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AMF-Mediated samarium tolerance in Avena sativa: Insights into primary metabolism, amino acid biosynthesis, and flavonoid accumulation

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Abstract

Samarium (Sm), a rare earth heavy metal, poses significant threats to plant health and productivity. In oat plants, elevated Sm exposure reduced grain yield by up to 60% and decreased photosynthetic efficiency by 43.2–60%. This decline in photosynthesis led to reduced growth due to energy deficiencies. Sm stress also caused metabolic imbalances and oxidative stress. Inoculation with arbuscular mycorrhizal fungi (AMF) mitigated these negative impacts. AMF symbiosis reduced Sm accumulation in plant tissues, improving grain yield by up to 33.9%. AMF also maintained photosynthetic activity, limiting its decline to only 2.5%. This was reflected in enhanced primary metabolism, with increased glucose and starch synthase activity providing better sugar availability. AMF stimulated the synthesis of amino acids (e.g., phenylalanine, arginine), organic and fatty acids. The activation of nitrogen metabolism enzymes like GS and GDH further supported the synthesis of these amino acids. Subsequently, these increased amino acids acted as vital precursors for secondary metabolites, notably flavonoids, phenolics and tocopherols (increased by 24.2–33.6%). By restoring nutrient levels and modulating metabolic pathways, AMF effectively mitigated Sm's detrimental effects, contributing to plant recovery and metabolic flexibility under stress. Overall, AMF inoculation enhanced plant resilience to Sm stress.

Introduction

Samarium (Sm), a member of the rare earth elements (REEs), is a lanthanide metal with a silvery sheen and moderate hardness. Though less renowned than some of its counterparts, Sm holds critical industrial and technological relevance. It is a fundamental component of samarium-cobalt (SmCo) magnets, known for their superior thermal stability and corrosion resistance. Sm is also employed in microwave and radar systems, nuclear reactors, and electronic devices such as capacitors and resistors [1, 2]. In the biomedical field, the radioactive isotope Sm-153 is used as a radiopharmaceutical in the palliative treatment of bone metastases, where it targets afflicted tissues with localized radiation while relieving skeletal pain [3]. Despite its technological and medical significance, the rising demand for Sm has led to increased environmental deposition through mining, electronic waste, and industrial effluents. Though Sm naturally occurs at low concentrations in the environment, anthropogenic activities have elevated its presence in soil and water systems, raising ecological and health concerns [4, 5]. Sm contamination near mining areas and e-waste zones disrupts soil microbial diversity and poses significant risks to plant development. It may enter the food chain through plant uptake, leading to bioaccumulation in agricultural products and aquatic organisms, thereby raising concerns for human and animal health.

Exposure to Sm and other heavy metals can result in substantial physiological and metabolic disturbances in plants. For example, Sm exposure has been shown to inhibit seed germination and early seedling growth in species such as lettuce and wheat, with toxicity intensifying in a concentration-dependent manner [6, 2]. Elevated Sm levels impair photosynthesis, mainly by reducing chlorophyll a conten and induce oxidative stress. This oxidative imbalance is often accompanied by decreased activity of key antioxidant enzymes, including superoxide dismutase (SOD), peroxidase (POX), and polyphenol

oxidase (PPO), ultimately weakening the plant's defense capacity and growth performance. Beyond oxidative stress, heavy metals such as Sm profoundly affect plant primary metabolism, particularly sugar metabolism. Sugars are not only vital for energy but also serve as structural and signaling molecules. They provide carbon skeletons essential for the biosynthesis of amino acids, fatty acids, nucleotides, and a wide range of secondary metabolites, such as flavonoids, alkaloids, and phenolics. Under metal stress, plants often redirect metabolic fluxes toward the synthesis of osmoprotectants, antioxidants, and defense-related compounds. This metabolic reprogramming supports survival and detoxification but may also compromise normal growth and reproductive functions.

Oat (Avena sativa L.), a cereal crop known for its nutritional value and adaptability to harsh environmental conditions, is widely cultivated for both human consumption and livestock feed. It also serves as a cover crop that helps prevent erosion and enhances soil structure. However, like other crops, oats are vulnerable to soil contamination by heavy metals such as Pb, Cu, and Sm. Such contamination interferes with nutrient acquisition, damages cellular membranes, disturbs metabolic pathways, and impairs overall plant performance [7]. Therefore, mitigating the negative effects of heavy metals is critical for ensuring crop productivity and soil health. In this context, arbuscular mycorrhizal fungi (AMF) represent a promising biological strategy to enhance plant tolerance against heavy metal stress. AMF form mutualistic associations with the roots of nearly 80% of terrestrial plants, enhancing water and nutrient acquisition by expanding the root absorptive area through extensive hyphal networks [8]. In addition to their nutritional benefits, AMF improve plant resistance to abiotic stresses—including drought, salinity, and heavy metal toxicity by modulating plant metabolism, enhancing antioxidant defenses, and improving osmotic adjustment [9, 10]. AMF also contribute to soil structure stabilization and microbial community health, further reinforcing their role in sustainable agriculture [11]. Recent studies highlight the ability of AMF to reduce oxidative stress and metal toxicity in plants by enhancing the synthesis of detoxification-related compounds such as phytochelatins, glutathione (GSH), and metallothioneins. Moreover, AMF influence the metabolic balance by supporting sugar metabolism and supplying precursors for biosynthetic pathways that build protective secondary metabolites, which are essential for stress mitigation and growth regulation. Given this background, our study investigates the potential of AMF to alleviate Sm-induced stress in oat (Avena sativa L.). We hypothesize that AMF inoculation will reduce Sm toxicity by enhancing physiological performance, stabilizing metabolic functions, boosting antioxidant defenses, and promoting the detoxification of Sm. This work aims to provide a deeper understanding of the synergistic interactions between AMF and oats under heavy metal stress, contributing to the development of sustainable strategies for managing contaminated soils.

Materials and methods

2.1. Plant growth and treatments

Sterilized soil and sand (Tref EGO substrates, Moerdijk, NL) were mixed in varying ratios (70–30%) with a 68% water-holding capacity. Oat seeds (Agricultural Research Center, Giza, Egypt) were surface sterilized using 5% sodium hypochlorite for 20 minutes. Seeds were planted in 10 × 8 cm pots filled with AMF-

treated or untreated soil. AMF inoculum (Rhizophagus irregularis) was applied 5 cm below the surface prior to seeding. The non-mycorrhizal control received equal amounts of autoclaved inoculum to ensure uniform nutrient availability. The soil contained 11.9 mg C, 12.8 mg NO_3-N, 1.3 mg NH_4-N, and 9.4 mg P per gram of dry soil, with 0.33 g water/g soil, EC of 3.4 dS/m, pH 7.56, and 2.75 meq/L K. Water content was maintained at 60%. Plants were grown in a climate-controlled chamber (21/18°C day/night, 16/8 h photoperiod, 150 µmol m^{-2} s^{-1} light, 60% humidity) and irrigated regularly with tap water. Five biological replicates were used per treatment in a randomized complete block design. After five weeks, biomass was measured, and samples were snap-frozen in liquid nitrogen and stored at − 80°C for biochemical analysis. Soil samples were stored at − 20°C. Six treatments were applied: 1) Control (0 mg Sm/kg soil), 2) AMF only, 3) Sm (125 mg/kg), 4) Sm (250 mg/kg), 5) AMF + Sm (125 mg/kg) and 6) AMF + Sm (250 mg/kg). Sm doses were selected based on a pre-experiment testing various concentrations (0–500 mg/kg soil), identifying 125 and 250 mg/kg as moderate and severe levels (causing 35% and 65% biomass reduction, respectively). Growth chamber conditions for the pre-experiment included 320 µmol m^{-2} s^{-1} light intensity, 60/70% humidity, 22/18°C, and a 16/8 h photoperiod. Biomass was recorded after four weeks, and samples were stored at − 80°C.

2.2. Determination of Sm

The concentration of Sm in plant extract was measured using inductively coupled plasma optical emission spectroscopy (ICP-OES) at a wavelength of 359 nm, employing Thermo Jarrell Ash 25 and PerkinElmer Optima 3200 RL instruments (PerkinElmer, USA).

2.3. Yield and photosynthesis

We measured the seed size, the weight of 100 seeds, and the number of grains per plant after the experiment was complete. The LI-6400 (LI-COR, Lincoln, The Netherlands) photosynthesis thesis system was used to calculate the photosynthesis. The LI-COR leaf chamber was utilized under the following parameters: block temperature of 22 ◦C, saturation photon flux density of 1500 µmol m − 2 s − 1, and 400 or 620 ppm CO2. Chlorophyll a and b extracted with acetone were measured [12]. In an enzymatic cycle between glycerol-3-phosphate oxidase and dehydrogenase, 3-phosphoglycerate, or 3-PGA, is evaluated by the non-radioactive test used to detect RuBisCo activity [13].

2.4. Determination of organic sugars

50 mM TAE buffer (pH 7.5) containing a blend of polyclar (0.15%), Na azide (0.02%), PMSF (2 mM), mercapto-ethanol (1 mM), mannitol (10 mM), and NaHSO was used to extract the soluble sugars. The mixture was heated to 90 ◦ 3 ◦ (12 mM) and centrifuged at 15,000 g. C for 10 minutes), then C for 5 minutes, and finally room temperature incubation. For five minutes, the centrifugation was repeated at 14,000g and 4□C. The sugars were then rinsed using ddH2, and high-performance anion-exchange chromatography/pulsed amperometric detection was used to quantify the various sugars [14]. The techniques of [15] and [16] were used to calculate galactomannans.

2.5. Amino acids determination

To extract the amino acids, 100 mg of shoot samples were homogenized in 80% aqueous ethanol for 1 minute at 7000 g, spiked with norvaline, and centrifuged for 20 minutes at 14,000 × g and at 4°C. Following the clear supernatant's vacuum evaporation, the particle was re-suspended in chloroform. The supernatant was separated from the pellet suspended in chloroform and centrifuged again after the residual was extracted again using deionized water of HPLC quality. Using a Millipore microfilter with a 0.2 M pore size, the centrifuged aqueous phase (14,000 × g, 10 min) was filtered. A Waters Acquity UPLC-tqd system (Milford) and a BEH amide column were used to determine the quantity of amino acids [17]. Milligrams per gram of fresh weight were used to express the content.

2.6. Evaluation of the fatty acid profile

The procedure outlined by [18] was followed in the extraction and measurement of fatty acids. In short, methanol was applied to 100 mg of shoot samples at room temperature until they were discolored. The identification technique involved the use of a Hewlett Packard 6890, MSD 5975 mass spectrometer and an HP-5 MS column (30 m × 0.25 mm × 0.25 mm) for gas chromatography-mass spectrometry (GC/MS) examination. Codeine and nonadecanoic acids were then added as internal standards. To do the GC-MS analysis, Hewlett Packard 6890, MSD 5975 was used. The NIST 05 and Golm metabolome databases (http://gmd.mpimp-golm.mpg.de) were used to identify fatty acids.

2.7. Antioxidant Activities

The total antioxidant capacity was measured by centrifuging 100 mg of sprouts at 14,000× g for 25 minutes at 4 ◦C after shaking them in an 80% ethanol solution. Next, a reaction solution comprising 0.3 M acetate buffer (pH 3.6), 0.01 mM TPTZ (2,4,6-tripyridyl-s-triazine) in 0.04 mM HCl, and 0.02 M $FeCl_3$ was used to conduct the FRAP (Ferric Reduction Antioxidant Power) experiment. Using a standard curve, the total antioxidant capacity was reported as µmol Trolox equivalents per gram of plant extract. Furthermore, by combining extract supernatants with the DPPH (2,2-diphenyl-1-picrylhydrazyl) reagent and detecting the absorbance at 517 nm, the total antioxidant capacity was evaluated spectrophotometrically. Tocopherols were found in shoot tissues by HPLC analysis using the procedures described in [19]. A Particil Pac 5 µm column (250 mm long by 4.6 mm wide) was used to separate the tocopherols, and a Shimadzu system running under normal phase conditions in conjunction with a fluorometric detector (excitation at 290 nm, emission at 330 nm) was used to quantify the results.

Samples were crushed using Liquid-N_2 in a MagNALyser, and then many materials were extracted in 80% ice-cold ethanol (2 mL) for polyphenol and flavonoid analysis. In 80% ethanol (v/v), flavonoids and total phenolic contents were extracted. Following the Folin–Ciocalteu assay, the quantities of flavonoids and phenolics were measured using $AlCl_3$ calorimetric assays. A spectrophotometer (Shimadzu UV–Vis 1601 PC, Japan) was then used to assess the flavonoids [20] and polyphenols [21]. The standards for phenolics and flavonoids, gallic acid and quercetin, respectively, were given in milligrams per gram of fresh weight.

2.8. Elemental analysis

Minerals were extracted from plant samples using an ICP-MS (Antwerp University) based on a solution of HNO3 in H2O (5:1 v/v) according to the previously established technique [22] for soil mineral detection.

2.9. Statistical analysis

Data of all parameters were subjected to SPSS 16.0 program and expressed as mean±(SE). To evaluate the main and interactive effects of Sm and AMF as fixed variables, two-way analysis of variance (ANOVA) was applied. Differences among means of treatments were evaluated with Duncan's Multiple Range test and significance was set at $P < 0.05$. Figures and heatmap were generated by GraphPad Prism 8.

Results

3.1. Effect of different treatments on samarium content, seed yield and photosynthesis

Sm content in oat plants increased with kts increases in soil, while AMF alleviated Sm increases in oat plants by 21.7% and 31.5% under lower and higher Sm concentrations, respectively (Table 1). Grain size, weight, and quantity were negatively impacted by both lower and larger amounts of Sm. Grain size, weight, and number decreased by 24.1%, 33.1%, and 28.5%, respectively, at the lower concentration of Sm; however, the higher concentration showed greater decreases in these parameters than the lower concentration. The results indicated that AMF significantly improved the negative effect of Sm on various yield parameters in oat plants compared to those treated by Sm only. In this regard, the AMF application enhanced seed size, weight, and grain number by 26.7%, 33.9%, and 28.8%, respectively, in comparison to those treated by Sm only at a lower concentration (Table 1). Furthermore, AMF reduced the adverse effects of the treatment by higher Sm concentration by 21.1%, 28.3%, and 16.6% for grain number, weight, and seed size, respectively. Moreover, photosynthetic rate measures revealed a non-significant decrease by 2.5% in AMF-treated plants compared to untreated plants ($p < 0.05$). Although this photosynthetic rate was significantly lower (− 43.2% and − 60%) compared to control plants under the treatments by Sm only at lower and higher concentrations, respectively (Table 1).

Table 1

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on samarium content in seeds, yield parameters and photosynthesis at harvest of oat plant. Values are mean of three replicates (n = 3) ± SE. Values with different letters, within the same row, are significantly different at $p \leq 0.005$.

Parameter	**0**		**125 Sm**		**250 Sm**	
	(-) AMF	**(+) AMF**	**(-) AMF**	**(+) AMF**	**(-) AMF**	**(+) AMF**
Sm content (µg g^{-1} DW)	0 ± 0^{a}	0 ± 0^{a}	46 ± 4^{b}	36 ± 1^{b}	111 ± 11^{d}	76 ± 2^{c}
Seed size	13 ± 0.55^{c}	14.1 ± 0.97^{c}	10.2 ± 0.33^{b}	13 ± 0.73^{c}	7.5 ± 0.23^{a}	9.1 ± 0.96^{ab}
Weight of 100 seeds (g)	1.54 ± 0.13^{c}	1.53 ± 0.11^{c}	1.03 ± 0.03^{b}	1.38 ± 0.09^{c}	0.74 ± 0.03^{a}	0.95 ± 0.08^{ab}
Grain NO. per plant	346 ± 28^{c}	347 ± 24^{c}	247 ± 8^{b}	318 ± 19^{c}	177 ± 3^{a}	207 ± 10^{ab}
Photosynthesis at harvest time	10.17 ± 0.69^{d}	9.913 ± 0.45^{d}	$5.769 \pm 0.37b^{c}$	6.886 ± 0.86^{c}	3.959 ± 0.15^{a}	4.977 ± 0.16^{ab}

Table 2

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of minerals of oat plant. Values are mean of three replicates (n = 3) ± SE. Values with different letters, within the same row, are significantly different at $p \leq 0.005$.

Parameter	0		125 Sm		250 Sm	
	(-) AMF	(+) AMF	(-) AMF	(+) AMF	(-) AMF	(+) AMF
Minerals (μg g^{-1} DW):						
P	44 ± 5.2^{b}	40 ± 2^{ab}	31 ± 1.1^{a}	49 ± 5.3^{b}	39 ± 1.5^{ab}	39 ± 1.5^{ab}
S	126 ± 8.9^{cd}	110 ± 2.8^{bc}	95 ± 1.7^{b}	133 ± 13.5^{d}	69 ± 3.5^{a}	94 ± 2^{b}
K	450 ± 63^{c}	405 ± 20^{bc}	339 ± 4^{ab}	439 ± 34^{c}	252 ± 6^{a}	269 ± 14^{a}
Mg	99 ± 8.3^{c}	99 ± 0.6^{c}	75 ± 0.7^{ab}	118 ± 8.8^{d}	63 ± 3.2^{a}	85 ± 0.9^{bc}
Ca	5.49 ± 0.48^{c}	6.26 ± 0.47^{c}	3.74 ± 0.07^{ab}	6.19 ± 0.32^{c}	2.7 ± 0.15^{a}	4.04 ± 0.55^{b}
Na	8.67 ± 1.39^{a}	6.75 ± 0.28^{a}	7.44 ± 0.32^{a}	8.45 ± 1.21^{a}	6.54 ± 0.34^{a}	6.53 ± 0.23^{a}
Zn	2.51 ± 0.26^{cd}	2.51 ± 0.09^{cd}	1.75 ± 0.05^{ab}	2.77 ± 0.28^{d}	1.3 ± 0.06^{a}	2.01 ± 0.05^{bc}
Fe	1.07 ± 0.09^{c}	1.08 ± 0^{c}	0.8 ± 0.01^{ab}	1.27 ± 0.09^{d}	0.67 ± 0.03^{a}	0.91 ± 0.01^{bc}
Cu	1.78 ± 0.17^{b}	1.29 ± 0.14^{a}	1.33 ± 0.03^{a}	2.26 ± 0.25^{c}	1.8 ± 0.06^{b}	1.96 ± 0.05^{bc}
Mn	0.125 ± 0.01^{ab}	0.09 ± 0.01^{a}	0.093 ± 0^{a}	0.158 ± 0.02^{b}	0.126 ± 0^{ab}	0.161 ± 0.02^{b}
Al	1.24 ± 0.18^{a}	1.06 ± 0.07^{a}	1.05 ± 0.05^{a}	1.44 ± 0.19^{a}	1.05 ± 0.04^{a}	1.09 ± 0.09^{a}

3.2. Effect of different treatments on antioxidant metabolites

Sm treatment decreased phenolic significantly by 9.6% at low concentration. While the higher concentration of Samaria caused a significant increase of 21.9% (Fig. 1a). AMF, when combined with Sm, significantly increased phenolics by 9.4% and 1/8% under the lower and higher concentrations of Sm, respectively. The flavonoid showed a nonsignificant change under a low concentration of Sm, either alone or when combined with AMF (Fig. 1b). In contrast, the high concentration of the Sm exhibited a

significant increase of flavonoids by 58.4%; this increase was alleviated by AMF (by 14.2%). AMF caused a significant decrease in FRAP by 17.5%, while Sm caused significant increases under both lower and higher concentrations by 9.4% and 26.1%, respectively (Fig. 1c). At the same time when AMF treated the stressed plants, FARP content significantly increased by 9% and 12.5% at low and high concentrations of Sm, respectively. DPPH and ABTS significantly increased under the treatment of AMF alone by 14.7% and 16.2% at low and high concentrations of Sm, respectively (Figs. 1d and 1e). The lower concentration of Sm showed significant decreases of DPPH and ABTS by 16.5% and 20.7%, respectively. In contrast, the high concentration of Sm caused a significant increase of DPPH by 77.3% and a non-significant increase in ABTS by 4.2%. AMF, when combined with Sm, caused a significant decrease of DPPH by 15.3% under the treatment by the higher concentration of Sm. Furthermore, as antioxidant compounds together clarify the physiological reactions of plants to biotic stress, the current study evaluated their content. The results indicated that in non-stressed plants, AMF application significantly enhanced phenolic compounds (by 17.0%), the DPPH (by14.7%) and ABTS (by 16.2%) compared to the non-treated plants ($p < 0.05$).

3.3. Effect of different treatments on tocopherol

AMF significantly increased alpha, gamma and the total tocopherol by 33.6%, 24.2% and 24.8% respectively (Fig. 2). The low concentration of Sm caused a non-significant decrease in alpha and beta tocopherol by 13.1% and 33%. In contrast, it caused significant increases of gamma and total tocopherol by 18.6% and 13.8%, respectively. The high concentration of Sm showed a significant increase of alpha tocopherol by 34.7% and a non-significant increase for each of beta, gamma and the total tocopherol. When AMF combined with either the low concentration or the higher concentration of Sm it caused a non- significant increase in alpha tocopherol and significant increases in beta, gamma and the total tocopherol by 30.8%, 14.3% and 17.9%, respectively (Fig. 2).

3.4. Effect of different treatments on glucose, starch, amylase and starch synthase

AMF caused a significant increase in glucose content by 25.5% and non-significant increase in starch content by 7.3% (Fig. 3a, b). Both lower and higher concentration of Sm exhibited significant increases of glucose content by 77.2% and 68.2%, respectively. No significant changes were recorded in starch content when stressed by Sm concentration, either by lower or higher concentration. AMF when combined with lower concentrations of Sm caused significant decrease by 16.7% and significant increase by 32.3% under the higher concentration of Sm. The treatment by lower concentration of Sm alone caused significant decrease in amylase enzyme 20.6%, while the treatment by the higher concentration of Sm exhibited non-significant decrease by 3%. The treatments by AMF either alone or combined with lower and higher Sm concentration caused significant increases in starch synthase by 59.8%, 20.5% and 19.6%, respectively when compared to the untreated plants.

3.5. Effect of different treatments on organic acid content

AMF alone caused significant increases of lactate, citrate, succinate, and oxalate by 34%, 33.2%, 34.6%, and 21.3%, respectively (Fig. 4). The treatment by lower concentrations of Sm caused a significant decrease in lactate, citrate, and succinate by 11.7%, 11.6%, and 12.1%, respectively. The treatment by the higher concentration of Sm exhibited significant increases in lactate, citrate, and succinate by 29.6%, 28.2%, and 31.2%, respectively. The treatments by AMF, when combined with either a lower or higher concentration of Sm, caused significant increases in lactate by 89.2% and 62.6%, respectively, when compared to those plants that were treated with Sm only. The same trends were exhibited in the case of citrate and succinate (Fig. 4).

3.6. Effect of different treatments on amino acids composition

Amino acids are important markers of plant stress responses and adaptations because they are direct byproducts of nitrogen metabolism. Significant variations in amino acid composition were noted in both stressed and non-stressed circumstances (Fig. 5). When oat plants grow under stress from Sm, the level of several measured amino acids (12 out of 20) increased significantly in comparison to the plants that were stressed. Twelve of the twenty amino acids that were tested increased when treated with AMF alone; asparagine, alanine, and histidine showed the largest increases. Most of the measured amino acids showed more increases under the treatment of the higher concentration of Sm alone than those under the treatment of the lower concentration of Sm. When AMF was applied to both treatments of Sm, the amounts of several amino acids significantly increased in comparison to the plants that were not treated. The study highlighted the elevated levels of alanine, threonine, tyrosine, and arginine, which showed increases of approximately 135.2%, 50%, 30%, and 32.3%, respectively, under treatment by Sm only (lower concentration) compared to control plants. The prior amino acids rose by 54%, 37.5%, 56.6%, and 54.9%, respectively, when exposed to a higher concentration of Sm. Valine and phenylalanine exhibited significant decreases under all treatments (Fig. 5r, s).

3.7. Effect of different treatments on nitrogen metabolism

To ascertain its possible contribution to improving plant resilience and metabolic responses in oat under both stressed and non-stress conditions by Sm, the effects of AMF treatment on GS and GDH were assessed (Fig. 6). The activity of GS was non-significantly increased by12.5% under both treatments of AMF alone and the treatment by the low concentration of Sm, while GDH increased significantly by 84.8% under the treatments of AMF alone and showed no significant change under the treatment by Sm alone. Additionally, treatment with AMF alone significantly boosted GDH activity by 84.4% (Fig. 6b). The treatments by both low and high concentration of Sm alone caused no significant changes of GDH.

3.7. Effect of different treatments on fatty acids

Generally, treatment by AMF only increased all measured fatty acids except dodecanoic (C12:0). The highest increases were recorded by Docosanoic (C22:0), Hexadecenoic (C16:1) and Tetradecanoic (C14:0) by 47.8%, 36.4% and 30%, respectively (Table 3). The treatment by low concentration of Sm caused decreasing in all measured fatty acids. Thirteen fatty acids showed significant decreases while

the remaining 6 fatty acids showed non significantly decreases (Table 3). AMF alleviated the negative effect of Sm at low concentration and at the same time it caused a significant increase for 13 fatty acids in comparison to untreated plants (control). The higher concentration of Sm exhibited increases in six fatty acids levels and decreases the other 13 fatty acids. When AMF combined with the high concentration of Sm, it caused significant increases of eleven fatty acids, these increases were more than those caused by high concentration of Sm only (Table 3).

Table 3

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of fatty acids of oat plant. Values are mean of three replicates (n = 3) ± SE. Values with different letters, within the same row, are significantly different at $p \leq 0.005$.

Parameter	**0**		**125 Sm**		**250 Sm**	
	(-) AMF	**(+) AMF**	**(-) AMF**	**(+) AMF**	**(-) AMF**	**(+) AMF**
Fatty acids (ng g^{-1} DW):						
Dodecanoic (C12:0)	1336 ± 34^{a}	1321 ± 37^{a}	1116 ± 268^{a}	1166 ± 88^{a}	1329 ± 64^{a}	1117 ± 68^{a}
Tetradecanoic (C14:0)	149 ± 11^{a}	195 ± 7^{a}	137 ± 34^{a}	172 ± 4^{a}	167 ± 3^{a}	161 ± 25^{a}
Pentadecanoic (C15:0)	201 ± 7^{a}	206 ± 16^{a}	159 ± 41^{a}	193 ± 7^{a}	192 ± 10^{a}	208 ± 4^{a}
Hexadecanoic (C16:0)	2679 ± 59^{ab}	3268 ± 264^{ab}	2366 ± 615^{a}	3075 ± 259^{ab}	2721 ± 103^{ab}	3563 ± 313^{b}
Hexadecenoic (C16:1)	137 ± 8^{ab}	187 ± 14^{b}	72 ± 15^{a}	143 ± 15^{ab}	124 ± 7^{ab}	148 ± 2^{ab}
Hexadecadienoic (C16:2)	55.9 ± 3.4^{ab}	76.2 ± 5.6^{b}	29.4 ± 6.3^{a}	58.2 ± 6^{ab}	50.5 ± 2.8^{ab}	60.3 ± 0.6^{ab}
Hexadecatrienoic (C16:3)	48.2 ± 2.9^{b}	65.7 ± 4.8^{c}	25.3 ± 5.4^{a}	50.2 ± 5.2^{b}	43.6 ± 2.4^{b}	52 ± 0.6^{b}
Heptadecanoic (C17:0)	88 ± 4.6^{ab}	91 ± 3.6^{ab}	68 ± 16.4^{a}	89 ± 4.2^{ab}	91 ± 6.3^{ab}	96 ± 2.6^{b}
Octadecanoic (C18:0)	225 ± 12^{bc}	278 ± 17^{c}	140 ± 31^{a}	231 ± 19^{bc}	215 ± 12^{bc}	244 ± 1^{bc}
Octadecenoic (18:1)	9527 ± 452^{ab}	11839 ± 566^{b}	7007 ± 1516^{a}	9985 ± 638^{b}	10012 ± 501^{b}	9109 ± 848^{ab}
Octadecatrienoic (C18:3)	1787 ± 85^{b}	2226 ± 116^{b}	1284 ± 279^{a}	1817 ± 125^{b}	1803 ± 97^{b}	1723 ± 113^{ab}
Eicosanoic (C20:0)	110 ± 4.4^{ab}	188 ± 14.8^{c}	90 ± 20.7^{a}	195 ± 41.1^{c}	105 ± 4.6^{ab}	170 ± 14^{bc}
Eicosadienoic (C20:2)	109 ± 4.2^{bc}	121 ± 6.6^{c}	70 ± 16.1^{a}	122 ± 14.4^{c}	77 ± 2.6^{ab}	100 ± 12.6^{abc}
Docosanoic (C22:0)	71 ± 1^{ab}	105 ± 9.5^{d}	53 ± 9.2^{a}	91 ± 3^{bcd}	78 ± 5.9^{bc}	96 ± 3.7^{cd}

Parameter	0		125 Sm		250 Sm	
	(-) AMF	(+) AMF	(-) AMF	(+) AMF	(-) AMF	(+) AMF
Tetracosanoic (C24:0)	90 ± 8^{a}	101 ± 7^{a}	73 ± 20^{a}	92 ± 12^{a}	84 ± 7^{a}	81 ± 4^{a}
Tetracosenoic (C24:1)	42.4 ± 2.9^{ab}	58.1 ± 3.1^{c}	34 ± 8.1^{a}	53.1 ± 1.5^{bc}	40.1 ± 3^{ab}	46 ± 1.8^{abc}
Pentacosanoic (C25:0)	44.7 ± 1.6^{a}	60.8 ± 4.8^{b}	36.7 ± 7.4^{a}	47.6 ± 5.2^{ab}	43.1 ± 2^{a}	38.1 ± 2.7^{a}
Hexacosanoic (26:0)	48.9 ± 1.3^{ab}	63.4 ± 6.7^{b}	42.8 ± 8.3^{a}	44.1 ± 6.8^{a}	46.1 ± 2.2^{a}	35.8 ± 0.3^{a}

3.8. Effect of different treatments on mineral content in oat shoot

Since minerals are essential for plant physiological functions and stress responses, the mineral content of shoot tissues was evaluated in the current study (Table 3). The findings showed that Sm stress significantly decreased the mineral content of oat plants. Under low-Sm stress, the amounts of phosphorus, sulfur, potassium, magnesium, calcium, and sodium all went down by 28.2%, 24.7%, 37.2%, 24.6%, 31.8%, and 14.1%, respectively. In addition, the microelements Zn, Fe, Cu, Mn, and Al showed significant decreases of 48.2%, 25.3%, 25.2%, 25%, and 15.3%, respectively. Under high-Sm stress S, K, Mg, Ca, Na, Zn showed more reduction than those reported under low-Sm stress, while Cu and Mn increased by 1.12% and 8.3%, respectively. According to the current findings, AMF considerably reduced the detrimental impact of Sm-stress on mineral uptake; when paired with low concentrations of Sm, the mineral levels rose more than when Sa-stress only was applied. In addition to lessening the detrimental effects of Sm, AMF significantly raised P, S, Mg, Ca, Zn, Fe, Cu, Mn, and Al relative to the untreated plants (control) by 13.4%, 5.3%, 21%, 12.7%, 10.3%, 18.6%, 26.9%, 33.3% and 16.1%, respectively. Although the plant's mineral content increased when AMF was added to the high concentration of Sm, it was still below that of the untreated plants.

Discussion

Heavy metals, as enduring environmental contaminants, pose substantial risks to ecosystems and human health. Their excessive accumulation is particularly alarming because it can potentially upset ecological equilibrium, with agricultural systems especially susceptible to these detrimental consequences. Our study explores the phytotoxic effects of Sm on the growth as well as carbon and nitrogen metabolism of oat (Avena sativa L.) plants. More curiously, we hypothesize that inoculating oat plants with arbuscular mycorrhizal fungi (AMF) may mitigate the deleterious impacts of Sm, improving plant growth and metabolic activities. Widespread industrial activity hastens soil erosion, endangering the long-term viability of world agriculture. Sm, like many heavy metals, may bind to important plant

enzymes, preventing critical growth and metabolic activities from taking place [2]. The plant's capacity to gain light energy, its photosynthetic efficiency, and its overall output and productivity could all be negatively affected in response to this retardation in photosynthetic efficiency. A similar response was observed in citrus rootstock seedlings treated with La that exhibited a great reduction in growth and development by retarding chlorophyll and carotenoids levels, that finally caused chlorosis and toxicity [23]. Another study declared that Armoracia rusticana can uptake both La ant Tb by endocytosis, leading to their accumulation in the cells, retarding the cellular activities and greatly affecting plant metabolism [24]. To this end, the phytotoxic effect of REEs such as Sm on plant growth and development differs depending on their concentrations and plant species. Understanding these interactions is imperative to ensuring the sustainability of agriculture. Consequently, to mitigate the detrimental consequences of Sm on oat plants, we implement arbuscular mycorrhizal fungi (AMF). We found that AMF significantly mitigated the phytotoxic impact of Sm on photosynthesis and consequently the yield of oat plants. In accordance with our results, it was reported that AMF reduced Pd levels in the leaves of *Robinia pseudoacacia*, leading to great improvement in its photosynthetic pigments and hence biomass accumulation [25]. Additionally, the inoculation of *Vitis vinifera* resulted in a significant enhancement of its growth measures, photosynthetic machinery, and chlorophyll fluorescence attributes [26]. Likewise, Yan et al. [27] observed that inoculating *Cinnamomum migao* with arbuscular mycorrhizal fungi (AMF) led to increased biomass and enhanced drought resistance by boosting the plant's physiological and metabolic functions. In line with this, AMF has shown the ability to alleviate the negative effects of heavy metal stress on plant growth and photosynthesis. This is achieved by improving nutrient uptake and limiting the accumulation of toxic metals in the above-ground parts of plants through a symbiotic relationship [28]. Additionally, AMF develops extensive hyphal networks that expand the root system's surface area, enabling more efficient absorption of water and nutrients—an advantage that supports plant health even under heavy metal exposure [11]. Notably, AMF can also immobilize heavy metals in the soil, decreasing their movement to leaves and shoots and thereby reducing toxicity that disrupts crucial functions like growth and photosynthesis [9]. In summary, AMF plays a key role in enhancing plant tolerance to heavy metal stress by facilitating nutrient acquisition and sequestering harmful metals. However, further investigation is needed to better understand its interactions with rare earth elements such as Sm, particularly in phytoremediation.

Heavy metal contamination in soils significantly threatens plant health by disrupting essential mineral nutrient uptake, transport, and balance. This interference may result in nutrient deficiencies, impaired physiological functions, and decreased crop productivity. Sm, a non-essential nutrient, can be absorbed by plants at high levels, potentially affecting plant nutrient uptake and physiological processes. Although the effects of Sm have not been as extensively studied as those of other rare earth elements, few studies have investigated the impact of Sm on interfering with plant mineral nutrition. In this respect, it was found that wheat plants exposed to Sm showed its accumulation in various parts, suggesting that it can be taken up and translocated within the plant system [2]. The accumulation of Sm may interfere with the uptake of essential nutrients by competing for binding sites or altering membrane permeability. Moreover, it may lead to deficiencies in vital elements such as Ca, Mg, and Fe, affecting plant growth and

development. This could be attributed to the chemical properties of heavy metals that may interfere with the essential elements, impairing their uptake by plants. For instance, Cd exhibits comparable chemical properties to zinc (Zn) and calcium (Ca), resulting in competitive inhibition and diminishing the uptake of such elements [2]. Further, Cd exposure reduces the uptake and translocation of essential elements such as Fe, Mg, and Mn, crucial for chlorophyll synthesis and photosynthesis. This competition affects the availability of nutrients and their distribution, leading to deficiencies and impaired metabolic processes [30]. Overall, heavy metal contamination disrupts plant mineral nutrition, necessitating strategies to mitigate stress and ensure sustainable crop production by understanding its effects on nutrient uptake and metabolism. The application of AMF greatly ameliorated the adverse effects of Sm on the uptake of minerals by oat plants. In this regard, AMF enhance plant mineral uptake under heavy metal stress by symbiotic association with roots, improving nutrient acquisition and mitigating heavy metal toxicity through various mechanisms [28]. The root hyphal networks were expanding by AMF, increasing absorptive surface area, and facilitating nutrient uptake. This is beneficial under heavy metal stress, as demonstrated by AMF inoculation in cadmium-contaminated soils, enhancing phosphorus acquisition, supporting better growth and development in plants [3]. Additionally, AMF immobilizes heavy metals in soil and fungal structures, reducing their bioavailability to plants by binding metals to fungal cell walls and sequestering them in vesicles [32]. Moreover, AMF secretes glomalin, a glycoprotein that improves soil structure and fertility by binding with heavy metals, reducing metal mobility, aiding detoxification, and promoting plant growth [33]. Furthermore, AMF immobilizes heavy metals and fungal structures, preventing metal leaching into groundwater and the food chain, making it valuable for bioremediation of contaminated soils [34].

Exposure to heavy metals, such as Sm, alters plant metabolism, specifically changing fatty acid and amino acid balances. These metabolic alterations are critical for plant adaptation and resistance to heavy metal stress. In this context, heavy metal stress in plants causes oxidative damage, leading to changes in fatty acid composition to maintain membrane integrity and fluidity [35]. Plants increase unsaturated fatty acids to maintain fluidity and maintain cellular functions. These changes also influence stress signaling pathways, activating defense mechanisms. On the other hand, amino acids, such as proline, play a crucial role in plant responses to heavy metal stress [36]. They act as osmoprotectants, antioxidants, and metal chelators, helping to stabilize proteins and membranes and reduce the toxicity of heavy metals. Specific amino acids can bind to heavy metals, reducing their toxicity by inhibiting their interaction with vital cellular components ([37]. In this regard, Ejaz et al. [38] highlighted that plants under heavy metal stress accumulate amino acids and other organic acids as part of their defensive mechanism. These metabolites help in detoxification and stress reduction. Additionally, the exposure to heavy metals such as Cu, Pb, and Cd affects the fatty acid composition of maize leaves, increasing saturated fatty acids while lowering unsaturated fatty acids, impairing membrane fluidity and integrity ([39]. On the other hand, AMF play an important role in reducing the negative effects of heavy metal stress on plant metabolism, notably amino acids and fatty acids. Their symbiotic relationship with plant roots increases the plant's resistance by influencing several physiological and biochemical processes. In this regard, plant contamination with heavy metals increases amino acid synthesis, including proline and

phenylalanine, which act as osmoprotectants and antioxidants, aiding in stress mitigation. AMF regulates amino acid metabolic pathways, promoting balanced accumulation for plant growth and stress resistance [40]. Moreover, AMF colonization alters plant fatty acid profiles, increasing unsaturated fatty acids, enhancing membrane fluidity and stability. This improves stress tolerance and protects against lipid peroxidation, reducing levels in plants exposed to heavy metals, thus protecting cellular structures from oxidative damage. In this context, it was reported that AMF greatly enhanced the tolerance levels of wheat plants when grown in soils contaminated with Europium (Eu) [41]. Likely, Abdelmoneim et al. [42] opined that AMF can play a pivotal role in ameliorating heavy metal stress in maize by improving their growth and metabolic activities by enhancing nutrient acquisition. Further, inoculation with AMF increased amino acids like L-asparagine, L-glutamine, and methionine, which are involved in glycine, serine, and threonine metabolism and arginine biosynthesis in *Medicago truncatula* plants grown in Cd-contaminated soils [31]. Treatment of *Malus hupehensis* with AMF under Cd-contamination conditions resulted in the upregulation of genes involved in amino acid biosynthesis and metabolism, enhancing the plant's antioxidant capacity and reducing cadmium-induced oxidative damage [26]. In conclusion, AMF strikingly mitigated the adverse effects of Sm upon the fatty acids and amino acids metabolism of oat plants.

Sugars and organic acids are essential for plant tolerance to heavy metal stress, acting as osmoprotectants, stabilizing cellular structures, scavenging reactive oxygen species, and chelating toxic metal ions [43]. In this respect, Cadmium exposure in rice seedlings increased total soluble and reducing sugar levels, decreased non-reducing sugars, and increased acid invertase and sucrose synthase activities, but decreased sucrose phosphate synthase activity [44]. Moreover, Arsenate exposure increased reducing sugars in rice seedlings, slightly increased starch content, and increased starch phosphorylase activity, while decreasing α-amylase activity [43]. Additionally, Cadmium stress was reported to inhibit sucrose phosphate synthase and sucrose synthase activities in the sucrose synthesis direction, while stimulating acid invertase and sucrose synthase in the hydrolysis direction [45]. Moreover, Pisum sativum exposed to Lead experienced a remarkable reduction in root development and altered enzymes involved in starch breakdown and sucrose metabolism, including α-amylase, β-amylase, sucrose phosphate synthase, and invertase [46]. Similarly, Aluminum toxicity reduced starch and sugar content in rice seedlings, resulting in lower α-amylase and invertase activity, impairing carbohydrate metabolism [47]. On the other hand, sunflower shoots and roots showed a remarkable increase in malic and citric acid levels due to exposure to aluminum and zinc, suggesting heavy metal detoxification through chelation and sequestration [48]. Plant roots release organic acids, which may impact heavy metal mobility in soil. These acids may decrease metal sorption, improve solubility, and boost bioavailability, influencing the absorption and transport of heavy metals in plants [49]. On the other hand, inoculation of oat plants greatly modulated the metabolism of sugars and organic acids to cope with Sm contamination. In this regard, Wand and Wu [50] highlighted the role of AMF in modulating sugar metabolism, including sucrose synthesis, transport, and metabolism, under heavy metal stress conditions. More interestingly, AMF was reported to improve heavy metal tolerance in plants by regulating sugar and organic acid metabolism [51]. Additionally, AMF greatly affect the accumulation of

organic acids and sugars, which play a pivotal role in chelating heavy metals and maintaining cellular homeostasis [28]. To this end, AMF significantly mitigates the adverse effects of Sm toxicity on oat growth and yield. It enhances nutrient uptake, supports physiological stability, and reduces Sm accumulation in sensitive tissues. This symbiotic association modulates the carbon and nitrogen metabolism, supports biomass accumulation, and enhances oat resilience under rare earth element stress like Sm contamination.

Conclusion

Our study investigated how Sm stress affected oat plants and how arbuscular mycorrhizal fungus (AMF) helped to mitigate it. Sm buildup has a negative impact on key growth and physiological characteristics such as seed production, photosynthesis, antioxidant levels, metabolism, and mineral content. However, AMF dramatically reduced the harmful impacts across most metrics. Sm exposure led to significant decreases in grain size, weight, and number, particularly at higher doses. In contrast, AMF increased these yield parameters, even under Sm stress, and partly recovered photosynthetic activity. While Sm alone resulted in unbalanced antioxidant responses (e.g., decreased phenolics at low doses and increased flavonoids at high concentrations), AMF stabilized these responses and boosted antioxidant capacity (DPPH, ABTS). In terms of metabolic components, AMF boosted glucose and starch synthase activity, which helped with energy management under stress. It also altered organic acid concentration and increased amino acid accumulation, especially under high Sm stress, suggesting better nitrogen metabolism and stress tolerance. AMF increased major nitrogen-related enzymes (GDH and GS), strengthening its significance in plant metabolism. Furthermore, AMF increased the production of tocopherols and essential fatty acids while mitigating Sm-induced decreases. It also greatly enhanced macro- and micronutrient absorption and retention, including phosphorus, potassium, magnesium, calcium, and iron, which were previously decreased due to Sm stress. Overall, AMF provided substantial protection against Sm toxicity in oat by increasing physiological, metabolic, and biochemical resistance. These results highlight AMF's potential as a long-term solution for reducing rare earth element-induced crop stress.

Declarations

a. Ethics approval and consent to participate: Not applicable

b. Consent for publication: Not applicable

c. Availability of data and materials: All data generated or analysed during this study are included in this published article.

d. Competing interests: The authors declare that they have no competing interests.

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and review. N.M.E.: methodology. S.M.K: software, validation. N.H., Y.S.A.: Writing - review & editing. M.G.M.: Writing - review & editing. A.A.S: Writing - review & editing. M.M.Y.M. and M.N.: validation, supervision, Writing - review & editing.

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Figures

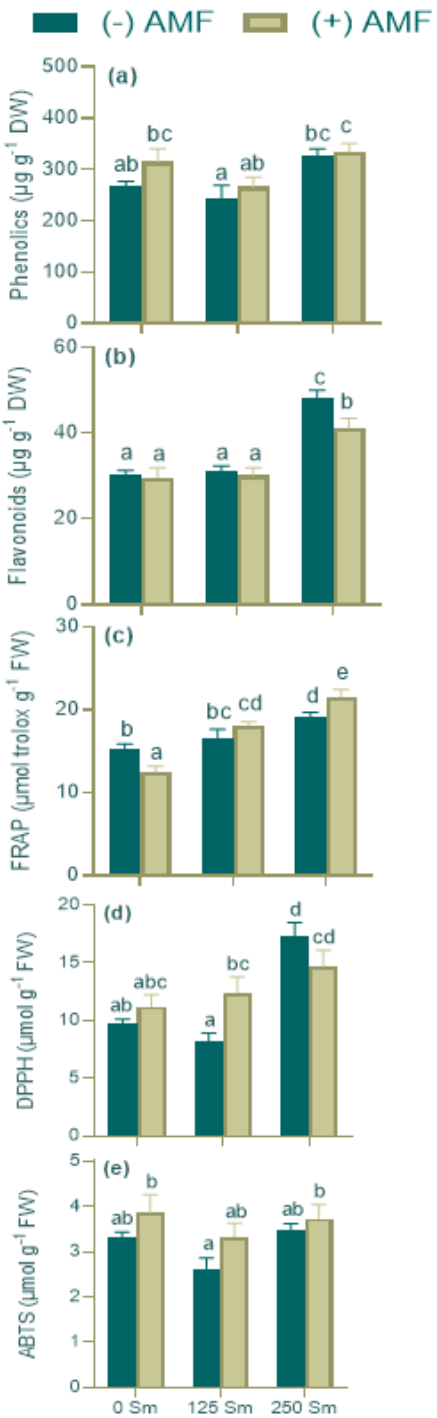


Figure 1

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of (a) Phenolics and (b) flavonoids, as well as (c) FRAP, (d) DPPH and (e) ABTS antioxidant capacity of oat plant. Bars are mean of three replicates (*n*=3) ±SE. Bars with different letters are significantly different at $p \leq 0.005$.

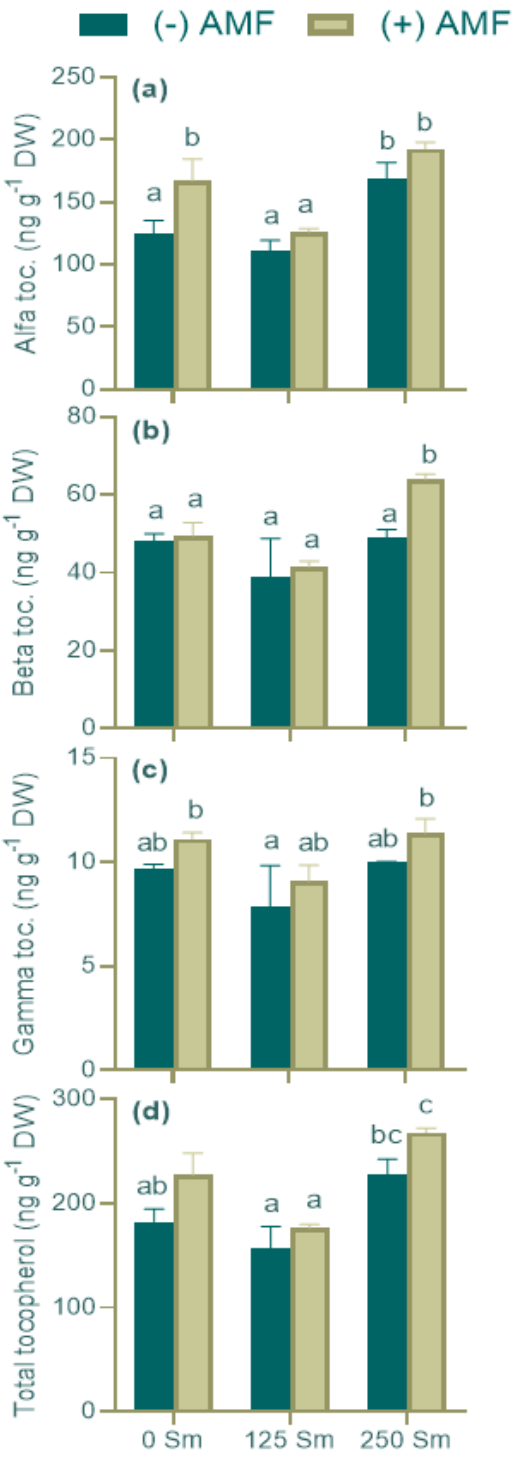


Figure 2

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of (a) alfa tocopherol, (b) beta tocopherol, (c) gamma tocopherol and (d) total tocopherol of oat plant. Bars are mean of three replicates (*n*=3) ±SE. Bars with different letters are significantly different at $p \leq 0.005$.

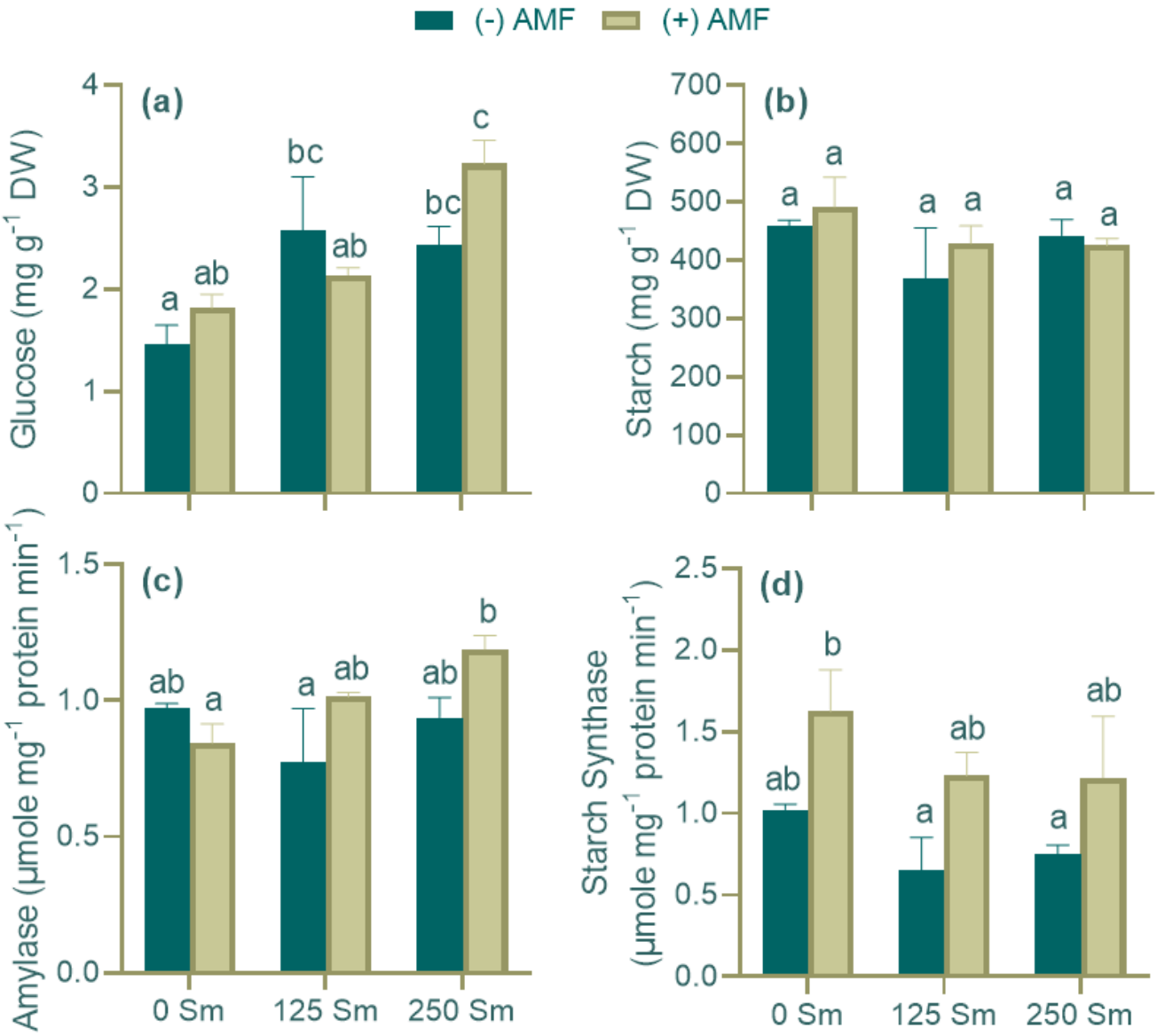


Figure 3

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of (a) glucose, (b) starch, (c) amylase enzyme and (d) starch synthase enzyme of oat plant. Bars are mean of three replicates (*n*=3) ±SE. Bars with different letters are significantly different at $p \leq 0.005$.

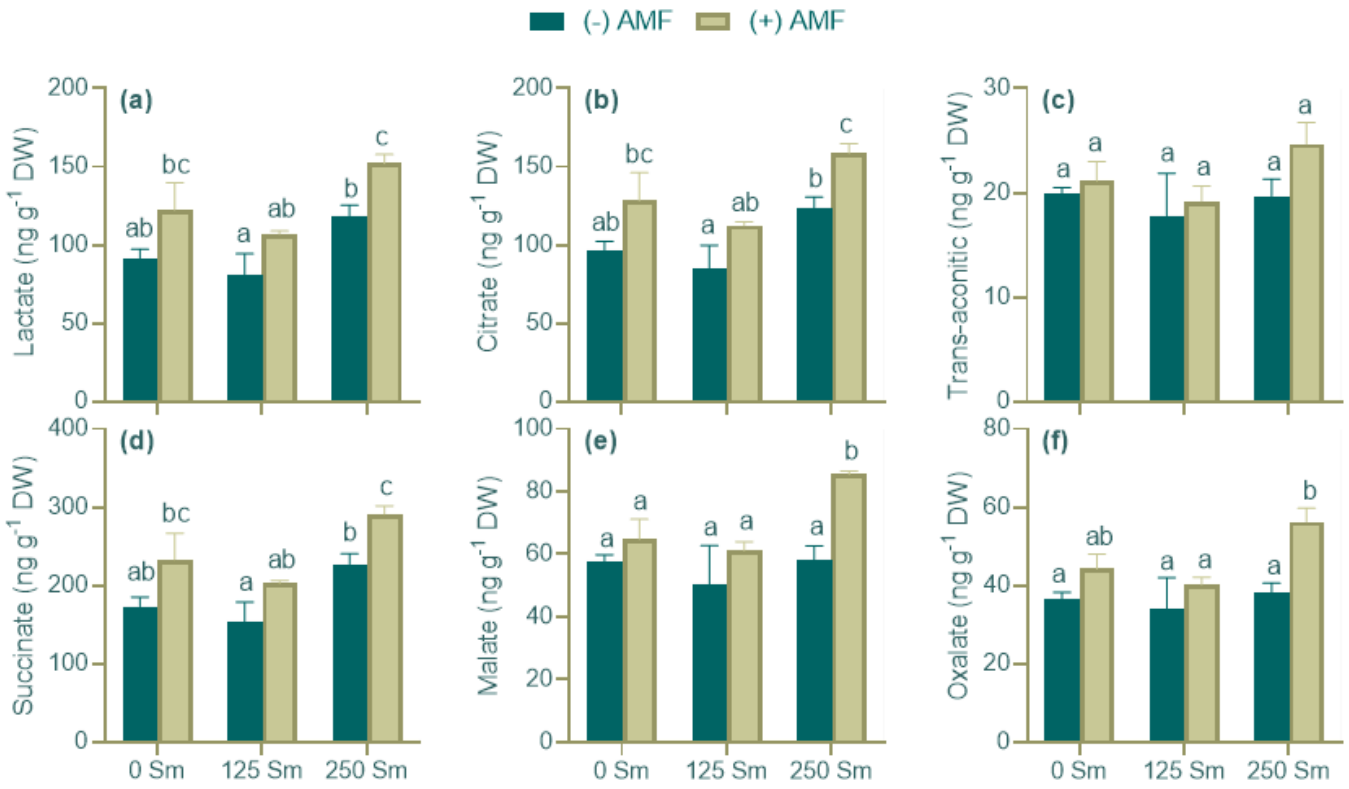


Figure 4

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of (a) lactate, (b) citrate, (c) trans-aconitic, (d) succinate, (e) malate and (f) oxalate of oat plant. Bars are mean of three replicates (n=3) ±SE. Bars with different letters are significantly different at $p \leq 0.005$.

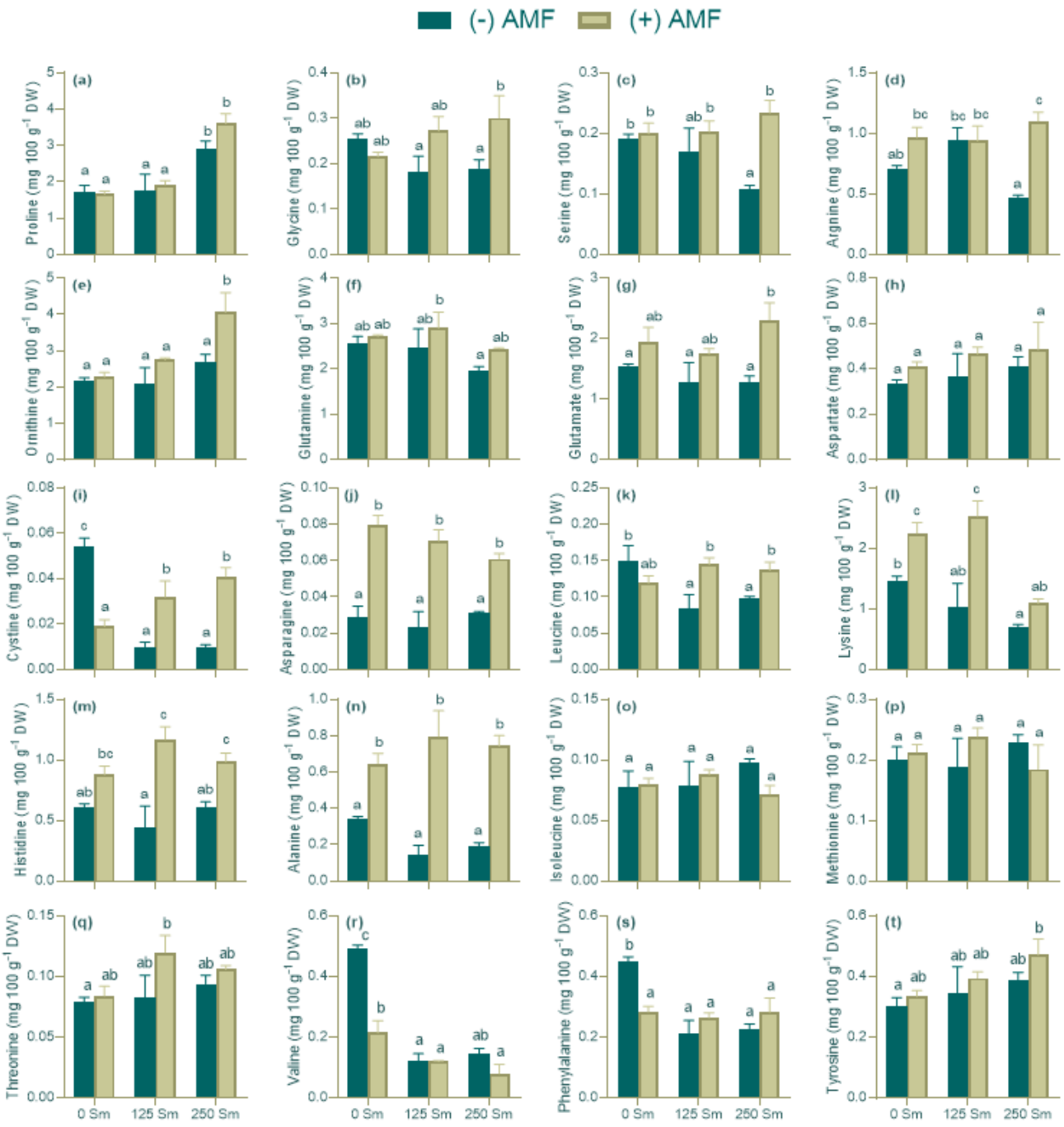


Figure 5

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of amino acids of oat plant. Bars are mean of three replicates (n=3) ±SE. Bars with different letters are significantly different at $p \leq 0.005$.

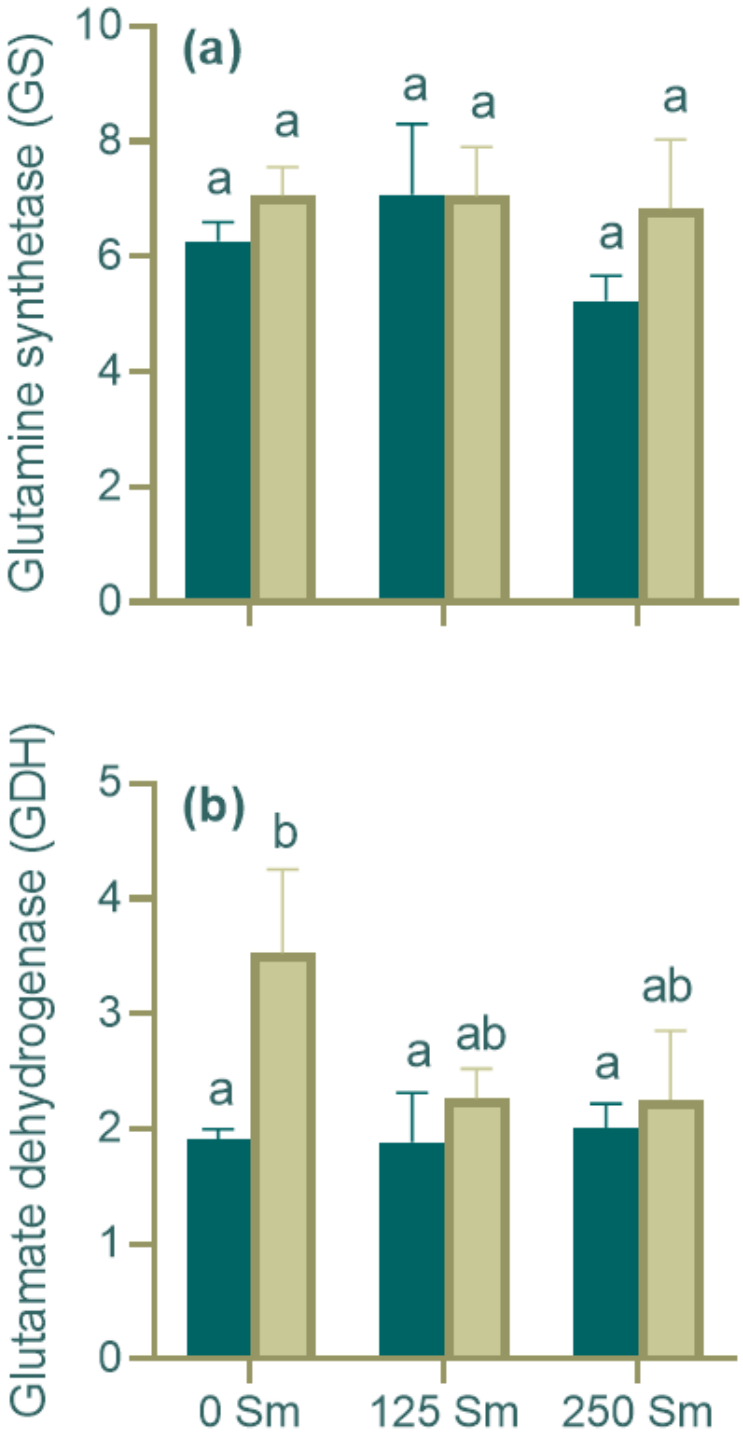


Figure 6

Effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of (a) Glutamine synthetase (GS) and (b) Glutamate dehydrogenase (GDH) of oat plant. Bars are mean of three replicates (n=3) ±SE. Bars with different letters are significantly different at $p \leq 0.005$.

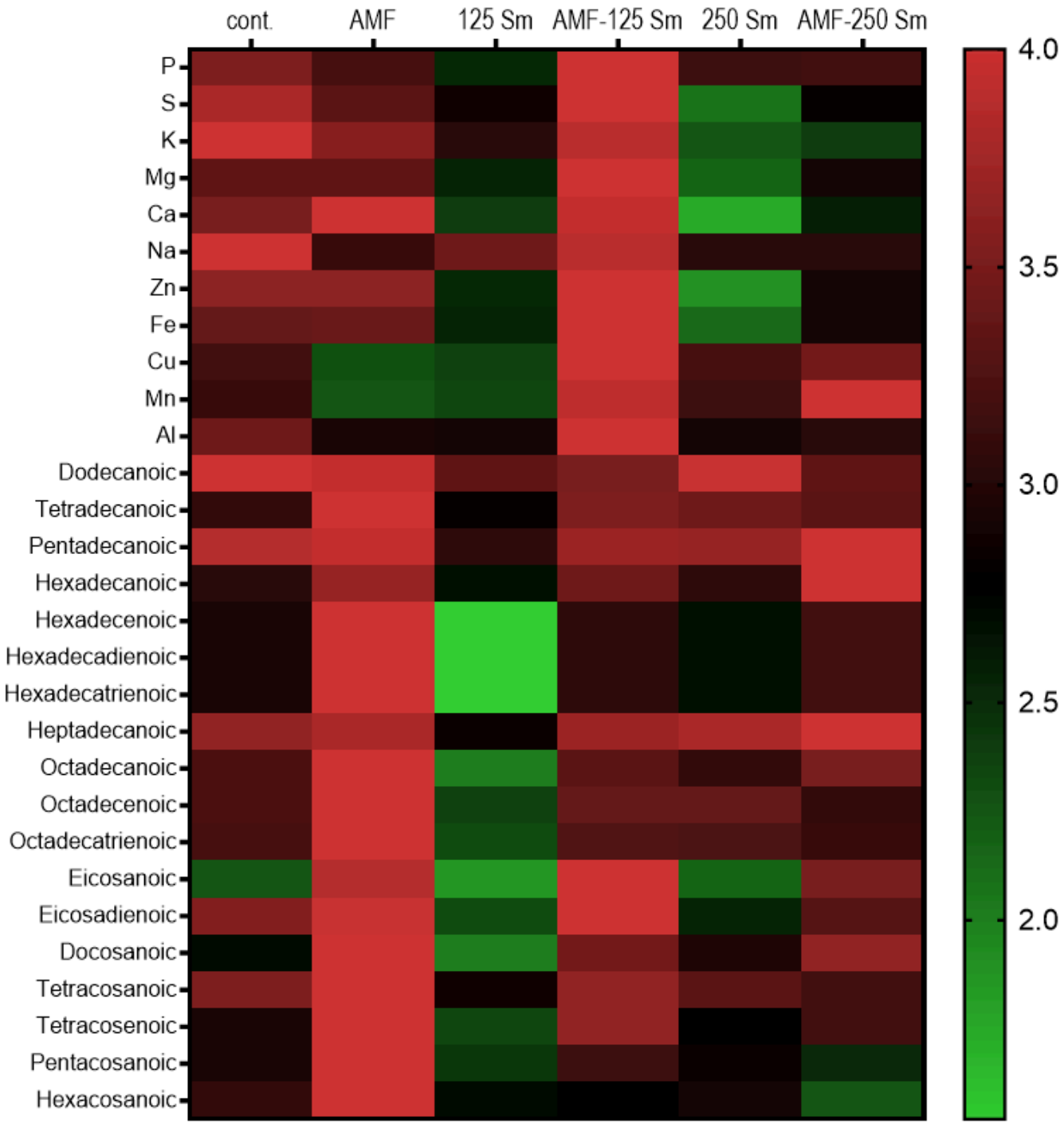


Figure 7

Figure 6. A heatmap showing the effect of different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF on content of minerals and fatty acids in seeds of oat plant.

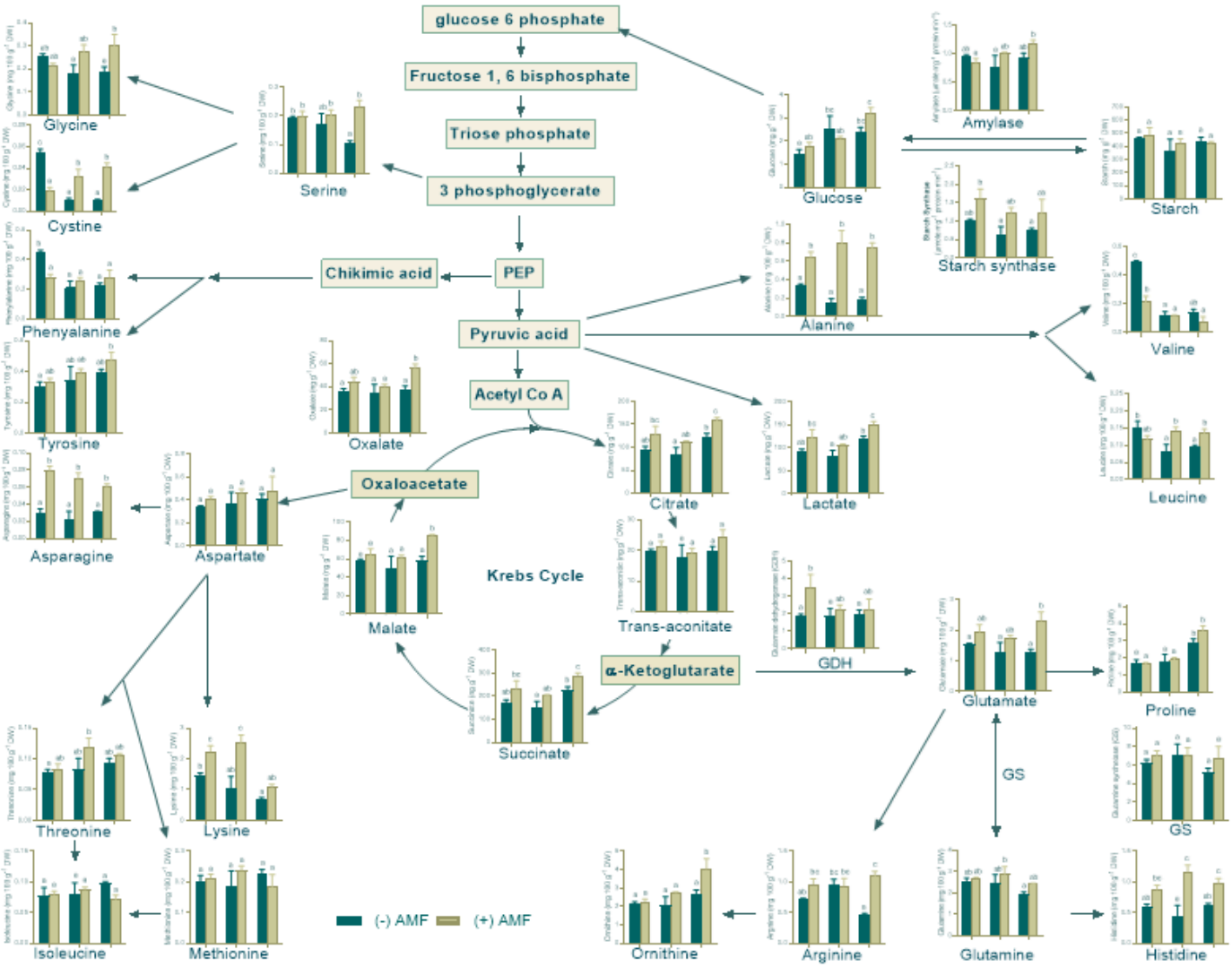


Figure 8

Figure 6. Change in different metabolites (sugars, organic acids and amino acids) in oat plant in response to different samarium concentrations (0, 125 and 250 mg kg^{-1} soil) and AMF. Bars are mean of three replicates (n=3) ±SE. Bars with different letters are significantly different at $p \leq 0.005$.

Supplementary Files

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- SupplementaryTable.docx