Received: 20 February 2024 | Revised: 13 April 2024 | Accepted: 20 April 2024

DOI: 10.1111/ppl.14328

ORIGINAL RESEARCH

Physiologia Plantarum

The fungus *Acremonium alternatum* enhances salt stress tolerance by regulating host redox homeostasis and phytohormone signaling

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Funding information
Ministerstvo Školství, Mládeže a Tělovýchovy, Grant/Award Numbers: 7AMB18DE015, 8J23DE004, 8X23011, CZ.02.2.69/0.0/0.0/19_073/0016670; Deutsche Forschungsgemeinschaft, Grant/Award Number: 390686111

Edited by U. Mathesius

Abstract

While endophytic fungi offer promising avenues for bolstering plant resilience against abiotic stressors, the molecular mechanisms behind this biofortification remain largely unknown. This study employed a multifaceted approach, combining plant physiology, proteomic, metabolomic, and targeted hormonal analyses to illuminate the early response of *Brassica napus* to *Acremonium alternatum* during the nascent stages of their interaction. Notably, under optimal growth conditions, the initial reaction to fungus was relatively subtle, with no visible alterations in plant phenotype and only minor impacts on the proteome and metabolome. Interestingly, the identified proteins associated with the *Acremonium* response included TUDOR 1, Annexin D4, and a plastidic K+ efflux antiporter, hinting at potential processes that could counter abiotic stressors, particularly salt stress. Subsequent experiments validated this hypothesis, showcasing significantly enhanced growth in *Acremonium*-inoculated plants under salt stress. Molecular analyses revealed a profound impact on the plant's proteome, with over 50% of salt stress response proteins remaining unaffected in inoculated plants. *Acremonium* modulated ribosomal proteins, increased abundance of photosynthetic proteins, enhanced ROS metabolism, accumulation of V-ATPase, altered abundances of various metabolic enzymes, and possibly promoted abscisic acid signaling. Subsequent analyses validated the accumulation of this hormone and its enhanced signaling. Collectively, these findings indicate that *Acremonium* promotes salt tolerance by orchestrating abscisic acid signaling, priming the plant's antioxidant system, as evidenced by the accumulation of ROS-scavenging metabolites and alterations in ROS metabolism, leading to lowered ROS levels and enhanced photosynthesis. Additionally, it modulates ion sequestration through V-ATPase accumulation, potentially contributing to the observed decrease in chloride content.

1 | INTRODUCTION

Microfossils, estimated to be more than 460 million years old, reveal intertwined fungal hyphae and spherical spores - evidence of endophytic coexistence dating back to when plants first colonized land. This discovery hints at a possible co-evolutionary journey between fungi and plants, one that began at the very inception of terrestrial life (Redecker et al. 2000). By residing within plants, endophytes contribute to a vibrant partnership, unlocking essential nutrients, stimulating production of growth hormones, siderophores or enzymes, and bolstering plant defenses against both harmful pests and diseases and abiotic stressors (Banaei-Asl et al. 2015; Gopalakrishnan et al. 2015; Khan et al. 2015; Afzal et al. 2019; Harsonowati et al. 2020; Marian et al. 2022; Verma et al. 2022). *Acremonium alternatum*, first described by Link in 1809, is a ubiquitous soil-borne filamentous fungus belonging to the Ascomycota phylum and *Hypocreaceae* family (Summerbell et al. 2011). *Acremonium*, a polyphyletic group encompassing over 150 diverse fungal species (Yao et al. 2019), has shown potential as a biocontrol agent against various plant pests and pathogens, including the diamondback moth larvae (Raps and Vidal 1998), powdery mildew (Romero et al. 2003), and *Plasmodiophora brassicae* (Auer and Ludwig-Müller 2023). Despite promising biocontrol potential, the precise molecular mechanisms underlying *Acremonium*'s interactions with plants and its potential role in mitigating abiotic stress remain largely unexplored. This highlights the need for further research in this area.

Among the most pressing abiotic challenges faced by arable lands is soil salinization (Seppelt et al. 2022). According to the information provided by the FAO soils portal, saline soils represented more than 424 and 833 million hectares of topsoil and subsoil, respectively, an equivalent of 25% of the worldwide agricultural land area (FAO, 2021). Soil salinization, driven by factors like rising temperatures, sea level rise, and agricultural practices (e.g., irrigation), is projected to significantly increase agricultural production losses, potentially jeopardizing staple food security (Nachshon 2018; Munaweera et al. 2022). While irrigated arable land in arid and semi-arid regions represents a crucial source of agricultural productivity, long-term irrigation itself poses a significant threat. Estimates suggest that 20–50% of irrigated land suffers from salinity, with toxic ion accumulation due to continuous irrigation leading to secondary salinization and annual losses of millions of hectares (Fita et al. 2015; Shahid et al. 2018; Jahan et al. 2020).

Soil salinity is a major threat to plant health, with the severity of its impact varying significantly due to species, specific genotypes, and inherent adaptability (Derbali et al. 2021). Furthermore, the adaptive response of plants to salinity is regulated by complex signaling networks and is also influenced by the plant's growth stage (Holsteens et al. 2022; Raza et al. 2023). Saline soils pose a multifaceted challenge to plant survival, triggering both osmotic and ionic stress responses. The osmotic gradient created by the salt impedes water uptake, leading to cellular dehydration and subsequent inhibition of cell expansion and division, ultimately stunting growth. Additionally, the accumulation of ions within the plant disrupts ionic homeostasis, damaging membranes, interfering with essential metabolic pathways like photosynthesis, and triggering the production of harmful reactive oxygen species that further contribute to cellular damage (Hao et al. 2021; Athar et al. 2022).

The focus of this work was to determine how *A. alternatum* contributes to oilseed rape's ability to tolerate salt stress during its early, vulnerable growth period.

2 | MATERIALS AND METHODS

2.1 | Fungal growth conditions, spore preparation and salt tolerance determination

Acremonium alternatum (MUCL No. 12012 of the culture collection at the Mycotheque de L'Université Catholique de Louvain, Belgium) was grown in liquid potato dextrose broth (HiMedia) on a rotary shaker (Innova 43, Eppendorf) at 25°C and 120 rpm for 10 days. The culture was then filtered using a pluriStrainer® (pluriSelect Life Science) to remove the mycelium, resulting in a pure spore suspension. The concentration of spores was subsequently determined using an improved Neubauer chamber (C-Chip – Disposable Haemocytometer, Labtech: Serving Scientists). To assess salt tolerance, *A. alternatum* mycelia were grown on potato dextrose agar (PDA) supplemented with a range of NaCl concentrations (0, 100, 200, 300, 400, 500, and 600 mM). Cultures were incubated at 25°C ± 2°C for three weeks. Mycelia were then imaged, harvested, lyophilized, and analyzed for chloride content (Cl^-) using six biological replicates.

2.2 | Plant growth and inoculation

Brassica napus L. seeds, cultivar Sázava, were obtained from the SEMPRA PRAHA a.s. breeding station in Slapy u Tábora, Czech Republic. The seeds were sown on pre-soaked and autoclaved Jiffy-7 peat pellets (Jiffy Sustainable Growing Solutions). These pellets were placed in magenta boxes (Steri Vent Containers, Duchefa) and plants were cultivated in a growth chamber under controlled conditions (20°C temperature, 300 µmol m^{-2} s^{-1} photon flux density, and a 16/8-hour light/dark cycle). After one week, seedlings received mock (10 mL of water), *Acremonium* (400 µL of an *A. alternatum* conidia suspension containing 10^7 spores ml^{-1} pipetted to the base of each seedling), salt (10 mL, 300 mM NaCl in water), or a combined *Acremonium*-salt treatment. Following a 72-hour incubation period (3 DAI), the NaCl and/or spore suspension treatments were repeated for each plant. Plants were imaged, and shoots were collected one week after the initial inoculation (7 DAI, growth stage 12, two leaves unfolded). For details, see Figure S1.

2.3 | Microscopy

Plant roots were washed thoroughly in running water, fixed in formalin-aceto-alcohol solution, and stored in a refrigerator at 4°C. To clear root samples, the fixative was removed and samples were placed in a mixture of 1% NaOH (w/v), 5% H_2O_2 (v/v), 2% sodium citrate

(w/v), and 0.03% $MgSO_4$ (w/v) in distilled water. The clearing mixture with root samples was heated to 60°C for one hour. Cleared samples were washed in distilled water, *Acremonium* hyphae were stained with a 0.1% solophenyl flavine 7GFE 500 fluorescent dye (Sigma-Aldrich, S472409-1G; visualisation of fungal cell walls, Hoch et al., 2005), and the samples were observed using a Leica DM4000 B fluorescent microscope (Leica Microsystems). Excitation and emission wavelengths were set to 400 and 470 nm, respectively.

2.4 | Proteome analysis

Freeze-dried plant shoot samples were homogenized using a Retsch Mixer Mill MM 400, and approximately 10 mg of homogenized tissue was extracted for omics analyses using a methyl tert-butyl ether/methanol/water mixture as described previously (Berková et al. 2022; Dufková et al. 2023). Portions of samples corresponding to 5 µg of peptide were analyzed by nanoflow reverse-phase liquid chromatography-mass spectrometry using a 15 cm C18 Zorbax column (Agilent), a Dionex Ultimate 3000 RSLC nano-UPLC system, and the Orbitrap Fusion Lumos Tribrid Mass Spectrometer (Thermo Fisher Scientific). The measured spectra were recalibrated and searched against the *B. napus* database (*B. napus* v2.0 – PRJNA237736) and common contaminants databases using Proteome Discoverer 2.5 (Thermo Fisher Scientific) with algorithms SEQUEST and MS Amanda (Dorfer et al. 2014). The settings were as follows: enzyme – trypsin, max two missed cleavage sites; MS1 tolerance – 5 ppm; MS2 tolerance – 0.1 Da, SEQUEST/0.02 Da, MS Amanda; fixed modifications – carbamidomethyl (Cys); dynamic modifications including Met oxidation, Asn/Gln deamidation; and dynamic modifications at the end of the protein – acetylation (N-end); loss of methionine (N-terminus); loss of methionine/acetylation (N-terminus). The chromatographic alignment and match between runs were generated by Feature Mapper (Chromatographic alignment: maximum RT shift 15 min, mass tolerance 10 ppm). The quantitative differences were determined by Minora, employing precursor ion quantification followed by normalization (total area) and calculation of relative peptide/protein abundances. The quantitative analysis centered on (i) proteins identified by two or more unique peptides and (ii) proteins with a single unique peptide but at least ten assigned peptides, aiming for broader proteome coverage. Protein function was predicted by searching sequences against the *Arabidopsis thaliana* proteome in STRING 11.0 (Szklarczyk et al. 2019) and UniProt (https://www.uniprot.org/). The mass spectrometry proteomics data were deposited at the ProteomeXchange Consortium via the PRIDE partner repository (Perez-Riverol et al. 2022) with the data set identifier PXD049437. The analysis was done with five biological replicates.

2.5 | Metabolome analysis

Polar and nonpolar fractions of metabolites separated in the initial step of protein extraction were derivatized and analyzed using a Q Exactive GC Orbitrap GC–MS/MS mass spectrometer (Thermo Fisher Scientific) coupled to a Trace 1300 Gas chromatograph (Thermo Fisher Scientific) as described previously (Berková et al. 2022, Berková et al. 2023). Samples for hormonal analyses were spiked with deuterated hormone analogue: [$^2H_6$] abscisic acid (Olchemim, Czech Republic) and processed as described before (Salem et al. 2020). Separation was performed using a TG-5SILMS column (30 m; 0.25 mm; 0.25 µm; Thermo Fisher Scientific) with a temperature gradient (5 min at 70°C followed by a 9°C gradient in 1 min to 320°C and final incubation for 5 min at 320°C). Helium was used as carrier gas at a constant flow rate of 1.2 mL/min. Metabolites were ionized using the electron ionization mode (electron energy 70 eV, emission current 50 µA, transfer line and ion source temperature 250°C). The MS operated in the full scan mode, 60000 resolution, scan range 50–750 m/z, automatic maximum allowed injection time with automatic gain control set to 1e6. Data were analysed by Compound Discoverer 3.3 (Thermo; peak detection settings—5 ppm; TIC threshold—10,000; S/N threshold—3) and searched against NIST2014, GC-Orbitrap Metabolomics library, and in-house library. Only metabolites that fulfilling identification criteria (score ≥75 and ΔRI <2%) were included in the final list of identified compounds. The quantitative differences were validated by manual peak assignment in Skyline 19.1 (Pino et al. 2020) using the extracted ion chromatogram (2 ppm tolerance). The analysis was done in five biological replicates.

2.6 | Anions analysis

Anions were extracted as previously described with few modifications (Aghajanzadeh et al. 2018); (Dietzen et al. 2020). To quantify water-soluble anions, approximately 15 mg of lyophilized and homogenized (Retsch Mixer Mill MM 400) plant or mycelial material was extracted by adding 1000 µL of sterile Milli-Q-water, incubated for 60 min at 4°C, and heated at 95°C for 15 min. Extracts were clarified by centrifugation (4°C for 15 min) and 100 µL of the supernatant was transferred into an ion chromatography vial and mixed with 900 µL of water. Anions were determined using a Dionex IonPac AS22 RFIC 4× 250-mm analytic column and ICS-1100 chromatography system (Thermo Scientific). The analysis was done with at least six biological replicates.

2.7 | Histochemical analyses

The distribution of hydrogen peroxide and superoxide radicals was determined as described previously, using 3,3′-diaminobenzidine and nitroblue tetrazolium, respectively (Berka et al. 2020). The GUS staining was performed using a transgenic *Arabidopsis thaliana* line 6 × *ABRE*::*GUS* and the protocol described previously (Berková et al. 2020) with minor modifications. Seedlings were grown under standard conditions for *Arabidopsis* in a growth chamber (AR36LX, Percival; 21°C/19°C day/night temperatures, with 16 h light/8 h dark photoperiods, 100 µmol m^{-2} s^{-1} photosynthetic photon flux density) on meshes (Uhelon 120 T, Silk & Progress) in Petri dishes with a half-strength Murashige and Skoog medium (Duchefa Biochemie) supplemented with 1.2% (w/v) agar (Duchefa Biochemie). Meshes with

one-week-old seedlings were transferred on the same medium supplemented with 150 mM NaCl and inoculated with *A. alternatum* (10 µL of spore suspension containing 10^7 spores ml^{-1} pipetted to the base of each seedling). Plants were collected after one week (7 DAI), vacuum infiltrated for 15 minutes with the staining buffer (0.5 M sodium phosphate, 1% (v/v) Triton X-114, 5 mM potassium ferricyanide, 5 mM potassium ferrocyanide, 1 mg ml^{-1} 5-bromo-4-chloro-3-indolyl-β-d-glucuronide, pH 7.0; Merck), incubated at 37°C for 2 h in staining solution, bleached in 70% (v/v) ethanol, imaged, and analyzed using ImageJ (Schneider et al. 2012).

2.8 | Statistics

The reliability of protein and metabolite identifications was assessed in Proteome Discoverer 2.5 (Thermo Fisher Scientific) and Compound Discoverer 3.2 (Thermo Fisher Scientific). STATISTICA, and MetaboAnalyst 6.0 (Lu et al. 2023) were used for statistical analysis (ANOVA, Fisher LSD, Kruskal-Wallis). The Student's t-test was calculated using MS Excel. For the Kruskal-Wallis and Conover test, the Real Statistics Resource Pack software for MS Excel was used (Release 6.8; Copyright 2013–2020; Charles Zaiontz; www.real-statistics.com). The reported statistical tests were generated and implemented using default and recommended settings unless otherwise indicated. PCA analyses were performed in ClustVist (Metsalu and Vilo 2015). Significant differences refer to $p < 0.05$ and adjusted adjusted $p < 0.05$ (The Benjamini-Hochberg procedure, 5% FDR).

3 | RESULTS

3.1 | *Acremonium alternatum* treatment primed stress response and indicated improved resilience to abiotic stress

The impact of *Acremonium alternatum* inoculation of seven-day-old *Brassica napus* seedlings was assessed after one week on multiple levels. The fresh and dry weights of shoots were comparable between control and inoculated plants under optimal growth conditions (for reference, see control plants in the following chapters). Similarly, the effects on the shoot proteome and metabolome were relatively mild. Metabolome analysis provided quantitative data for 141 metabolites spanning primary and secondary metabolic pathways (Table S1), with only three metabolites from the phenolic family showing a statistically significant impact of *Acremonium* inoculation, namely protocatechuic acid, trans-ferulic acid, and cis-caffeic acid (all less abundant in *Acremonium*-inoculated plants; adjusted $p < 0.05$). Proteome analysis yielded identification and quantitative data for 3,814 and 2,521 protein families, respectively. When comparing plants treated with *Acremonium* to the control group, we observed 88 differentially abundant proteins (DAPs; adjusted $p < 0.05$, absolute fold change >1.5), which represented less than 0.5% of the estimated protein content (Figure 1A; Table S2). DAPs accumulated in response to *Acremonium* were enriched ($p < 0.05$) in carbohydrate-active enzymes (CAZymes), protein metabolism and processing, and pyruvate and amino acid metabolism. A mild enrichment ($p < 0.1$) was found for glutathione metabolism, TCA, purine metabolism, and ribosomal proteins (Figure 1B). The detailed analysis of proteome data and information on

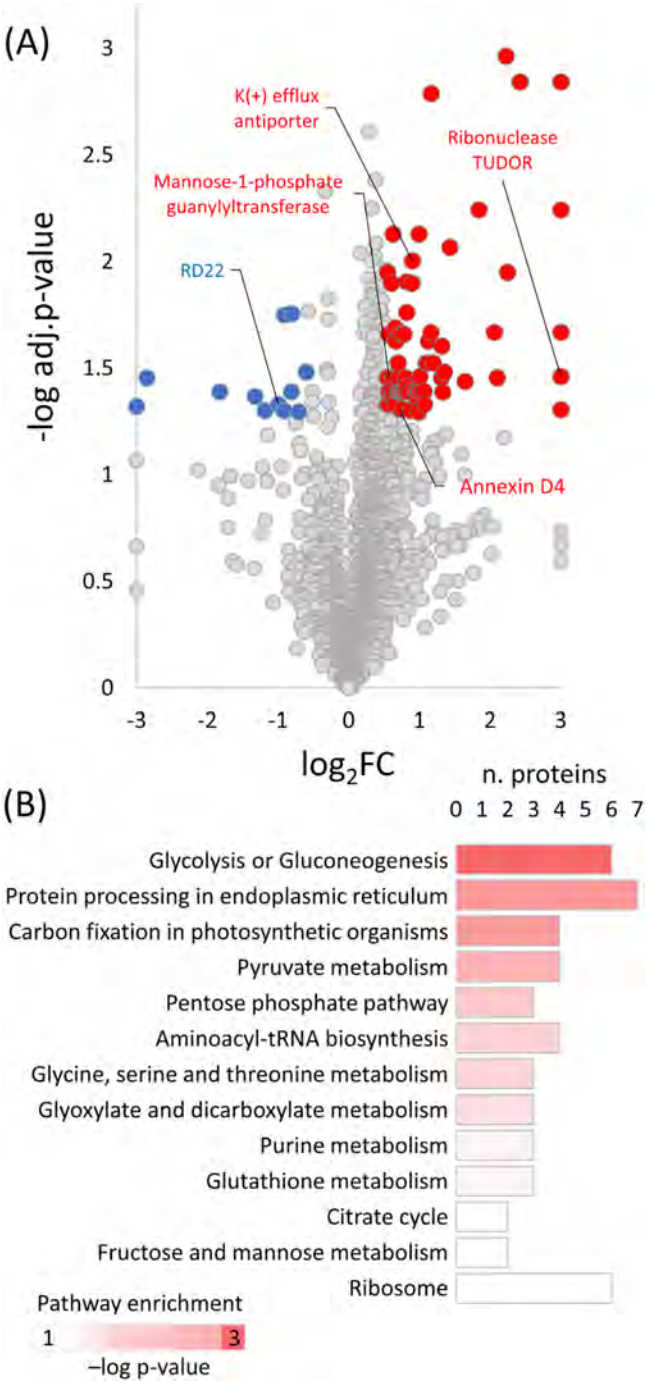

FIGURE 1 *Acremonium* response proteins in shoots of *B. napus* plants. (A) Differentially abundant proteins compared to mock-inoculated plants (adjusted p-value<0.05, relative FC >1.5, five independent biological replicates, each consisting of an independently grown plant) and (B) enriched metabolic pathways identified using MetaboAnalyst. The highlighted proteins are potential candidates responsible for promoted growth and resilience, as indicated by previously published analyses of corresponding mutant plants. For details, see Table S2.

corresponding orthologs in *Arabidopsis thaliana* pinpointed five *Acremonium* response proteins, namely (1) dehydrin-responsive BURP domain protein RD22 (decrease in abundance; abscisic acid-responsive, mutant displays an enhanced drought tolerance; Harshavardhan et al. 2014), (2) Mannose-1-phosphate guanylyltransferase (increase in abundance; involved in cell wall biosynthesis and ascorbate metabolism, loss-of-function mutant displays retarded growth, sensitivity to stress, and hypersensitivity to ammonium; Olmos 2006; Barth et al. 2010), (3) Annexin D4 (increase in abundance; mutant sensitive to osmotic stress and abscisic acid; Lee et al. 2004), (4) plastidic K^+ efflux antiporter (increase in abundance; single mutant does not have any visible phenotype, but double mutants in the gene family display reduced primary root length, a lower abscisic acid accumulation and impaired photosynthesis; Zheng et al. 2022), and (5) Ribonuclease TUDOR 1 (increase in abundance; required for resistance to abiotic stresses, slower growth under salt stress; (Yan et al. 2014). Taken together, these proteins indicated that *Acremonium* promoted processes that counter abiotic stressors, including responses to salt stress.

3.2 | *Acremonium* growth is not adversely affected by moderate or highly saline conditions

Before testing the resilience of *Acremonium*-inoculated plants to salt stress, the growth of *Acremonium* mycelium under saline conditions was evaluated. This test showed that *Acremonium* can grow in PDA media with up to 400 mM NaCl without any significant differences in growth rate compared to the control (Figure 2A-C). Interestingly, fungal growth was promoted in media supplemented with 100 mM NaCl (Figure 2A), and growth suppression at the highest NaCl concentrations was only 40% on average. This suggests that *Acremonium* growth is not adversely affected, even in strongly salinized soils with conductivity above 15 dS m^{-1} (equivalent to approximately 150 mM NaCl; Hardie and Doyle 2012; Polle and Chen 2015). Subsequent anion analysis showed a correlation between Cl^- content in the mycelium and the concentration in the medium (Figure 2C; Pearson's $r = 0.99$), suggesting that growth was likely not facilitated solely by the strict elimination of NaCl.

3.3 | *Acremonium* promotes the growth of rapeseed seedlings under salt stress

To explore the potential impact of *Acremonium* priming on salt stress tolerance, one-week-old seedlings were watered with 10 mL of 300 mM NaCl (corresponding to approximately 40% of the total Jiffy pellet water adsorption capacity) and inoculated with *Acremonium* spores as described in Materials and Methods (Figure 3A-D). The second NaCl treatment was done 72 hours after the initial treatment to maintain both water balance and salt stress. Additionally, inoculated

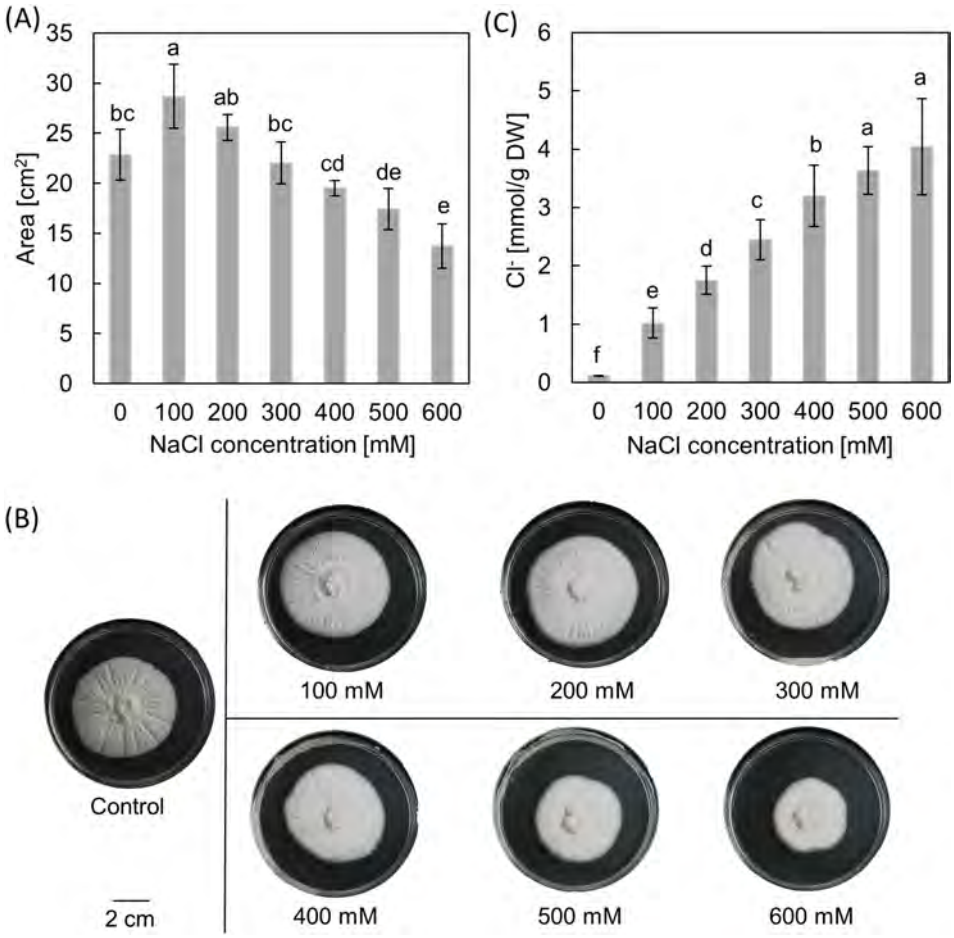

FIGURE 2 *Acremonium* growth in media supplemented with NaCl. (A) Mycelium area three weeks after inoculation and (B) corresponding representative images. (C) Accumulation of chloride ions in the mycelium. The plots represent the means and standard deviation of at least six independent biological replicates, each consisting of an independently grown mycelium. Letters represent statistically significant differences ($p < 0.05$; A, ANOVA, Tukey HSD test; B, Kruskal-Wallis and Conover test).

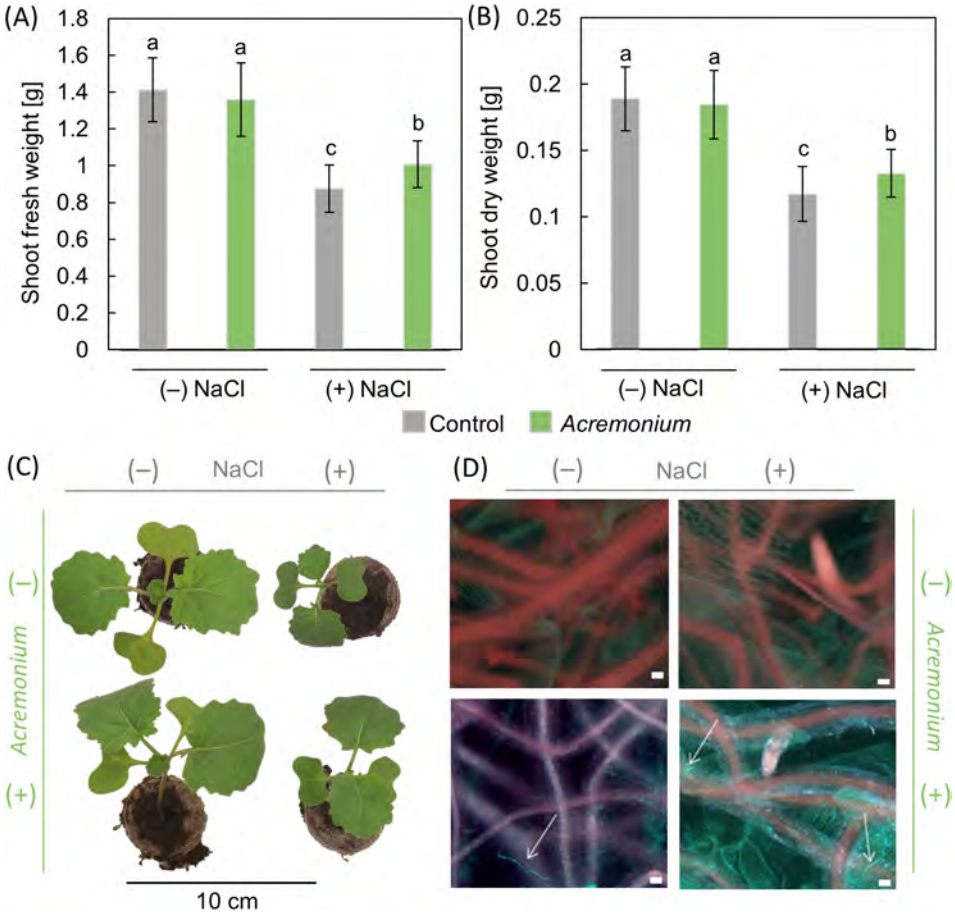

FIGURE 3 *Acremonium* priming promotes growth in plants under salt stress. Increase in the fresh (A) and dry (B) weights of the shoots under salinity stress. The bars represent means and standard deviations (n > 25 independently grown plants for each group), letters represent statistically significant differences ($p < 0.05$, ANOVA, Tukey HSD test). (C) Representative images of 14-day-old *B. napus* plants (7DAI). (D) Fluorescence microscopy images showing *Acremonium* surrounding the root system. Spores and hyphal fragments are marked with white arrows; red, roots; green, *Sphagnum* leaves (remnants from the peat substrate); scale bars represent represents 20 µm.

plants were re-inoculated to prevent *Acremonium* washout from the root zone due to the repeated watering. *Acremonium* is an endophytic fungus that colonizes the roots of its host plant. This well-documented phenomenon is particularly evident in the *Brassicaceae* family, including *B. rapa* (Jäschke et al., 2010) and *B. oleracea* (Raps & Vidal, 1998). Notably, the latter study suggests that *Acremonium* can eventually colonize the aerial parts of its host given sufficient time. In our experiments, *Acremonium* primarily formed loose associations around the root system (Figure 3D), with very limited colonization of *B. napus* tissue observed in only one plant from the microscopy samples (data not shown). Despite minimal colonization, *Acremonium* association significantly enhanced *B. napus* growth under salt stress. Under optimal conditions, both control and inoculated plants displayed comparable fresh and dry weights. However, under salt stress, inoculated plants exhibited significantly higher ($p < 0.05$) leaf area, fresh weight, and dry weight compared to non-inoculated plants, with increases of 12%, 13%, and 12%, respectively (Figures 3A-C and S2).

3.4 | The analysis of protein profiles further supported the mitigation of salt stress in plants co-treated with *Acremonium* and salt

Proteome analysis identified 300 and 275 DAPs in salt-treated plants and those treated with both salt and *Acremonium*, respectively (adjusted p-value <0.05, relative fold change >1.5; Table S2). Notably, *Acremonium* inoculation suppressed the response to salt for 157 DAPs, significantly attenuated the response of five DAPs (adjusted p-value <0.05), and reverted the response of two proteins: putative ribosomal RNA small subunit methyltransferase G and chloroplastic NADPH-dependent alkenal/one oxidoreductase. Principal component analysis (PCA) based on all identified DAPs (including *Acremonium* response proteins) revealed a significant difference between control plants and salt-stressed ones (separated in PC1), and further demonstrated that *Acremonium* inoculation partially restored the proteome of salt-stressed plants to that of controls (Figure 4A). The second principal component appeared to be driven by the response to *Acremonium* treatment and was significantly lower than the one associated with salt treatment. This observation aligns with the results of a two-way ANOVA, which confirmed statistically significant differences in the effects of the two factors, suggesting their distinct and non-proportional impacts on the proteome profile (Figure 4B). Intriguingly, a large portion of the DAPs responding to *Acremonium* remained unchanged when exposed to both *Acremonium* and salt (Figure 4C). Comparing enriched metabolic pathways driven by identified DAPs under salt stress revealed an overlap in amino acid metabolism, regulation of ribosomal proteins, protein processing in the endoplasmic reticulum, and processes related to photosynthesis and carbohydrate metabolism. However, *Acremonium* inoculation under salt stress appeared to uniquely affect glutathione metabolism, metabolism of

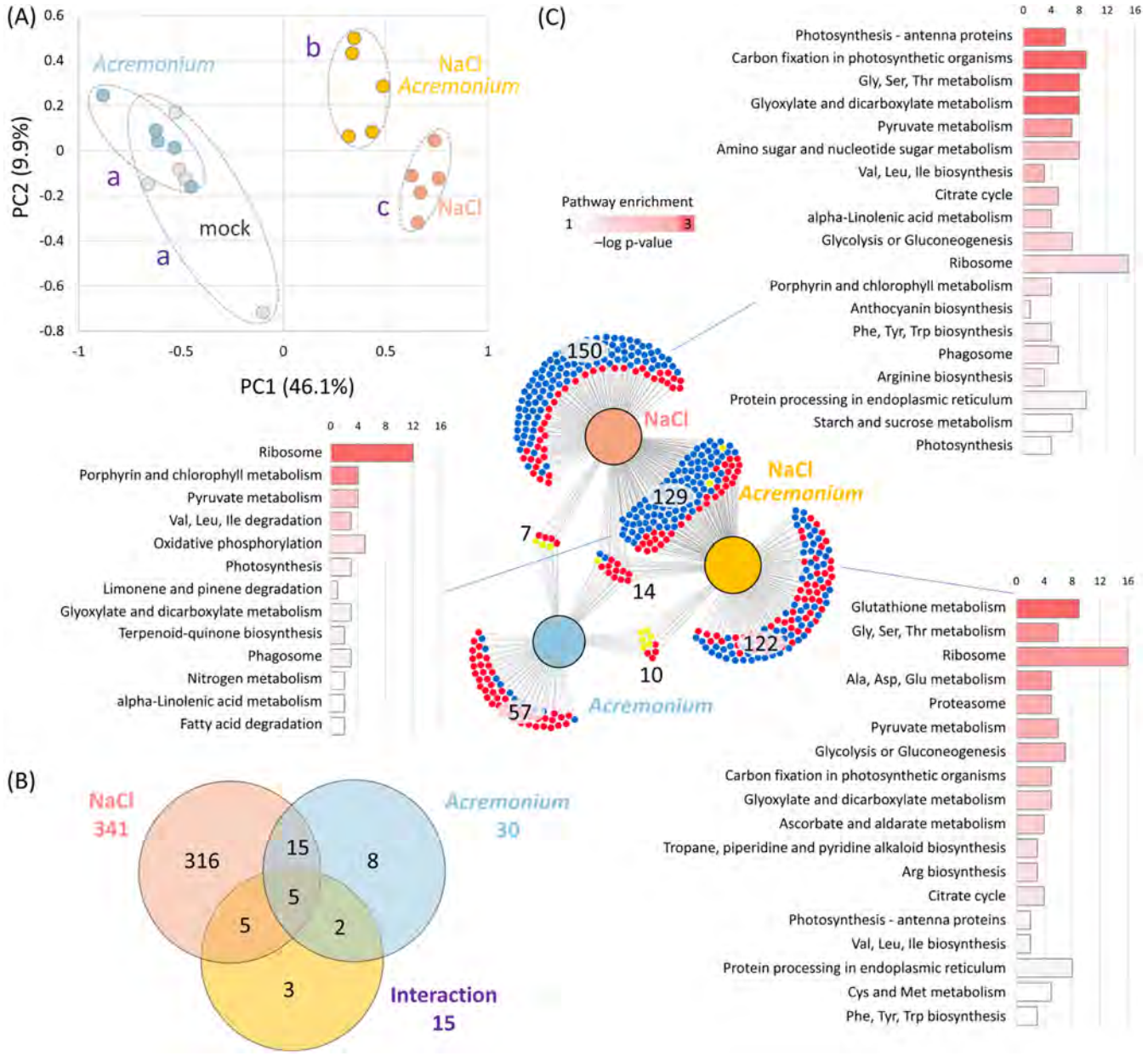

FIGURE 4 *Acremonium* priming significantly alters the proteome profile in *B. napus* under salt stress. (A) PCA separation based on 489 DAPs (adjusted p-value <0.05, relative fold change >1.5; Pareto scaling). Letters represent statistically significant differences according to Kruskal-Wallis and Conover's test ($p < 0.05$). (B) Two-way ANOVA results corroborate these findings, showing a significant impact (adjusted $p < 0.05$, no FC threshold) of salt stress (NaCl) and *Acremonium* on the number of DAPs, with only a limited interaction between these factors. (C) The DiVenn visualization depicts DAPs (adjusted p-value <0.05, absolute fold change >1.5) and significantly enriched metabolic pathways identified by MetaboAnalyst in DAPs specific to salt stress, *Acremonium*-primed plants under salt stress, and in the overlap of these two treatments. Red and blue dots indicate a relative increase and decrease in protein abundances compared to mock-treated control plants, respectively, while yellow dots represent differential responses between the comparisons (see Table S2 for details).

specific amino acids linked to nitrogen and sulfur assimilation (Ala, Asp, Glu, Cys, Met), the proteasome, and secondary metabolic pathways involving ascorbate and aldarate metabolism as well as tropane, piperidine, and pyridine alkaloid biosynthesis. Interestingly, while some metabolic pathways showed overlap between salt and salt-*Acremonium* treatments, others were unique to salt stress alone. Notably, only DAPs specific to salt-treated plants were enriched in pathways like amino sugar and nucleotide sugar metabolism, anthocyanin biosynthesis, and starch/sucrose metabolism (Figure 4C). Gene ontology analysis identified well-known salt-stress response proteins and genes (GO:0009651 response to salt stress) only present in DAPs from salt-treated plants, not found in those co-treated with *Acremonium*. These included two superoxide dismutase isoforms, an ortholog of a chloroplastic DEAD-box ATP-dependent RNA helicase involved in abscisic

acid regulation and salt stress response (AT5G26742; (Lee et al. 2013), an ortholog of prefoldin essential for NaCl tolerance (AT5G23290; (Rodríguez-Milla and Salinas 2009), and an ortholog of peroxygenase associated with stress signaling pathways (AT2G33380; (Partridge and Murphy 2009).

3.5 | *Acremonium* inoculation enhanced abscisic acid signaling and accumulation in plants under salt stress

The analysis of *Acremonium*-primed plants identified numerous proteins potentially acting downstream of abscisic acid signaling. Notably, beyond stress response proteins, the *Acremonium*-primed proteome exhibited an increase in the abscisic acid receptor PYL1 (1.8-fold, $p < 0.1$). Comparing plants treated with salt alone to those exposed to both *Acremonium* and salt revealed a substantial increase in an ortholog of Myrosinase 1, known for its involvement in abscisic acid response (AT5G26000; Islam et al. 2009) and an increase in SAL1, a negative regulator of abscisic acid signaling (AT5G63980; Xiong et al. 2001). These findings collectively suggest an *Acremonium*-mediated rise in abscisic acid signaling or content, which was subsequently confirmed by targeted phytohormone profiling (Figure 5A) and analysis of *Arabidopsis* reporter line 6 × *ABRE:GUS* (Figure 5B-D). The elevation in the abscisic acid pool induced by *Acremonium* was only evident under salt stress conditions (Figure 5A). However, the reporter line clearly demonstrated a significant enhancement in abscisic acid signaling within both roots and shoots upon *Acremonium* inoculation.

3.6 | Metabolome composition provided further evidence of alterations in secondary metabolism and amino acid biosynthesis in response to *Acremonium* under salt stress

To complement and corroborate the results of proteome profiling, the metabolome of *B. napus* was analyzed. Metabolites were separated into polar and nonpolar fractions and profiled using GC–MS analysis. More than 140 metabolites were reliably identified (Table S1). The results confirmed the expected significant impact of salt stress on both primary and secondary metabolites. However, in contrast to the proteomics data, the metabolome did not show a significant impact of *Acremonium* inoculation on the response to salt stress. A total of 70 and 69 differentially abundant metabolites (DAMs; relative fold change >2, adjusted p-value <0.05) were identified compared to the

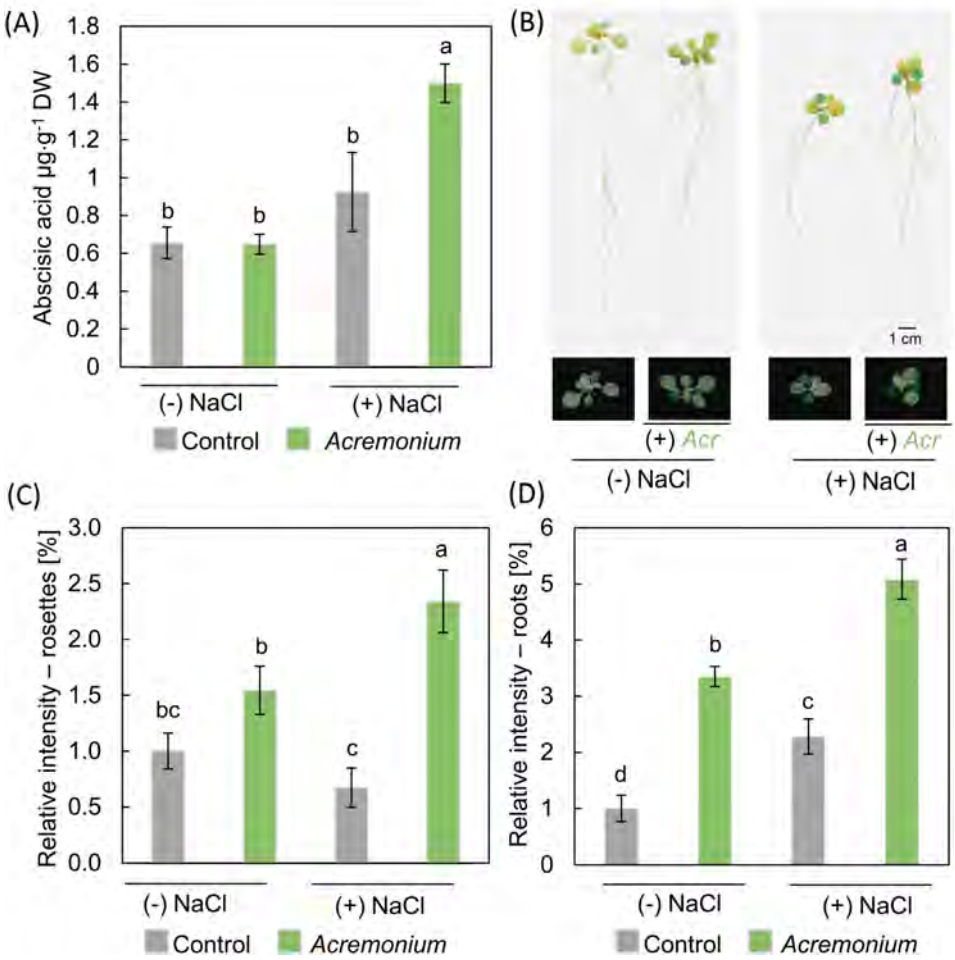

FIGURE 5 *Acremonium* infection impacts abscisic acid accumulation and signaling. (A) Endogenous abscisic acid levels in *B. napus* and (B-D) signaling determined using a 6 × *ABRE::GUS Arabidopsis* reporter line. Bar plots represent means and standard error (at least five independently grown plants for each group). Letters indicate statistically significant differences ($p < 0.05$, Kruskal-Wallis and Conover test). The signal intensity was normalized to the total leaf and root area for C and D, respectively.

control in plants treated with salt and those treated with both salt and *Acremonium*, respectively (Tables S1). While the majority of the 65 DAMs exhibited similar responses in both salt-treated and salt-*Acremonium*-treated plants, *Acremonium* inoculation exerted a protective effect against specific metabolic alterations induced by salt stress. Notably, it mitigated the salt-induced accumulation of phenylpyruvic acid (a precursor of phenylalanine and phenolics), cis-ferulic acid (a phenolic compound), xanthine, and histidine. Additionally, it prevented a decrease in 2-aminoadipic acid, a potential precursor of glutamic acid. In line with the observed enrichment of the Asp metabolic pathway (Figure 4C), *Acremonium* inoculation resulted in a decrease in oxoglutarate and aspartate. Furthermore, *Acremonium* inoculation led to an increase in nervonic acid and the phytoalexin brassinin. Notably, the increase in brassinin, a known compound involved in plant defense mechanisms, suggests a priming of the plant's biotic stress response (Tables S1).

3.7 | *Acremonium* inoculation promoted ROS metabolism

Acremonium inoculation under salt stress triggered alterations in enzymes and metabolites of glutathione metabolism, decreasing ROS detoxification components like catalase and superoxide dismutase (Figure 4C, Tables S1, S2). This, coupled with improved growth, suggested reduced ROS production. Histochemical staining and quantification confirmed this hypothesis, showing significant reductions in hydrogen peroxide (87%) and superoxide (70%) under salt stress with *Acremonium* inoculation (Figure 6A-D).

3.8 | *Acremonium* induced accumulation of V-type proton ATPase under salt stress

Proteomic analysis revealed quantitative data for 13 V-type proton ATPase subunits. Notably, all three identified catalytic subunits A significantly increased in abundance (adjusted $p < 0.05$) under combined salt and *Acremonium* treatment. Additionally, a moderate (1.3-fold) increase was observed for a potassium ion antiporter that was identified as a DAP induced by *Acremonium* priming (Figure 1A). These results implied an increase in ion sequestering, and indeed, anion analysis revealed a notable, statistically significant ($p < 0.05$) drop in chloride concentration in *Acremonium*-treated plants under salt stress (Figure 7A). Intriguingly, plants seemingly compensated for a 12% reduction in chloride by increasing dry weight, resulting in remarkably similar total chloride content per plant (0.22 mmol). This observation implies that efficient sequestration in *Acremonium*-treated plants, despite similar uptake, allows them to evade the growth attenuation observed under salt stress.

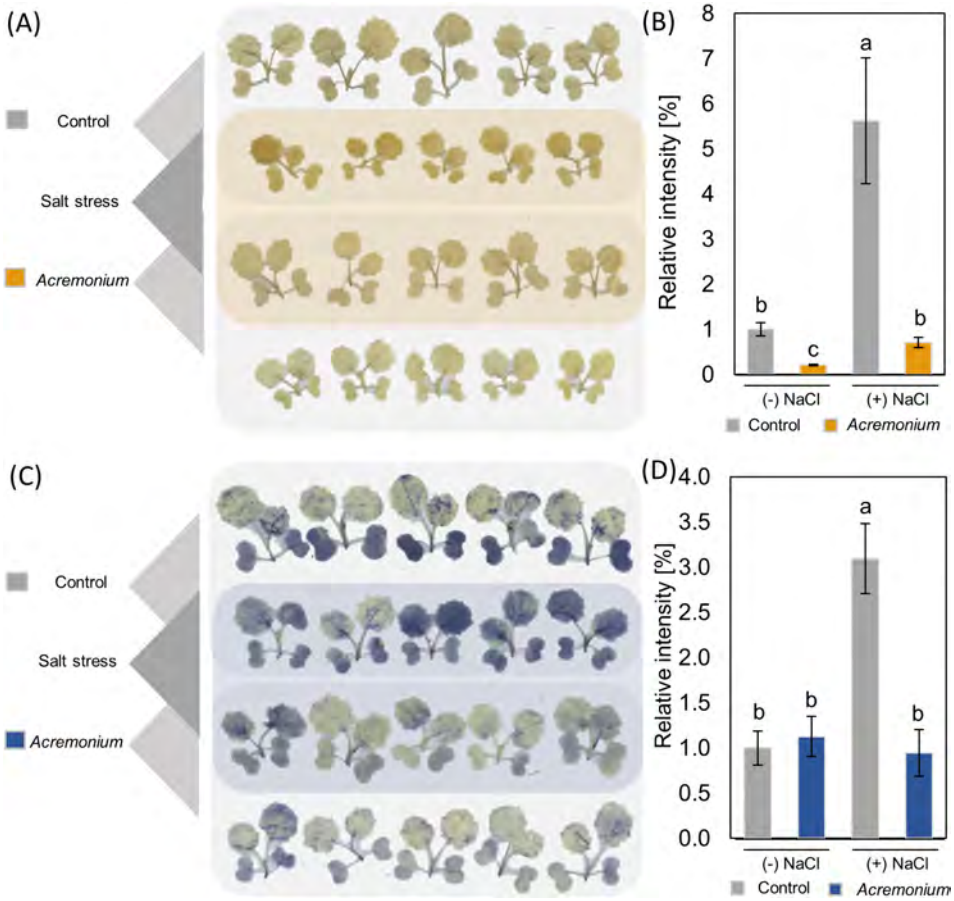

FIGURE 6 *Acremonium* inoculation reduces the amount of hydrogen peroxide and superoxide under salt stress. (A,B) Estimation of hydrogen peroxide content by DAB staining and (C,D) superoxide by NBT staining. Representative images of 14-day-old plants (7 DAI) and corresponding results of image quantitation. Bars represent means and standard error (12 independently grown plants for each group), letters represent statistically significant differences ($p < 0.05$, Kruskal-Wallis and Conover test). The signal intensity was normalized to the total leaf area.

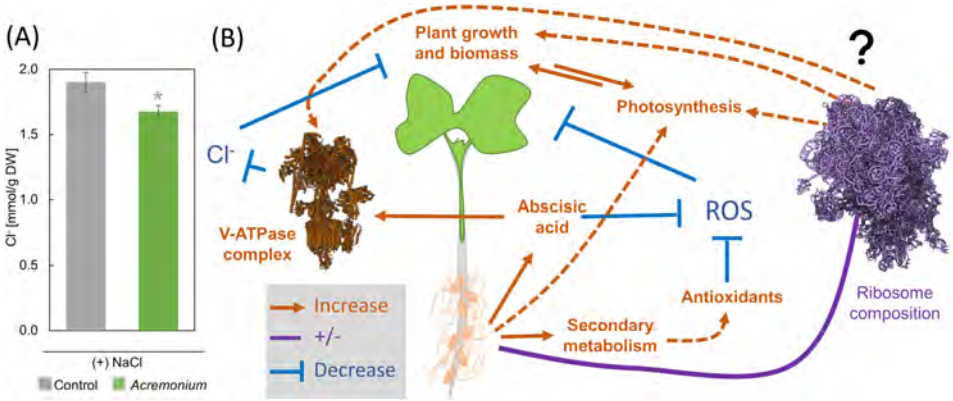

FIGURE 7 (A) Chloride ion accumulation in plants exposed to salt stress. Letters indicate statistically significant differences ($p < 0.05$, Student's t-test; six independently grown plants for each group). (B) A model depicting *Acremonium*-mediated growth promotion under salt stress. Details on the represented pathways and molecular processes are provided in the discussion and Tables S1 and S2. Protein 3D structures sourced from RCSB Protein Data Bank.

4 | DISCUSSION

4.1 | *Acremonium* - a halotolerant fungus boosting plant resilience to salt stress

Halotolerant fungi emerge as potent biotechnological tools for enhancing agricultural productivity in saline environments. Exhibiting remarkable tolerance to high salt concentrations, these fungi establish beneficial symbioses with plants, empowering them to withstand osmotic stress and maintain cellular homeostasis. Consequently, plants survive and thrive in previously unsuitable soils (Anand et al. 2023; Chauhan et al. 2024). The remarkable salt tolerance of *Acremonium alternatum*, evidenced by its largely unaffected mycelial growth even at concentrations exceeding those encountered in highly salinized soils (Figure 2A-C), aligns with its classification as a halotolerant fungus (Śliżewska et al. 2022). It is noteworthy that *Acremonium* exhibited a higher salt tolerance than established salt-tolerant biocontrol agents, such as *Trichoderma* and *Hypocrea* (Kashyap et al. 2020). Similar to established biocontrol agents, inoculation with *Acremonium* demonstrated a positive impact on salt tolerance in *B. napus* seedlings, resulting in an over 10% improvement in shoot dry weight under salt stress (Figure 3B). The experiments with *Arabidopsis thaliana* demonstrated that *Acremonium* also promoted the growth of this model plant under both control and salt stress conditions, leading to an increase in rosette area by an average of 24% and 15%, respectively (Figure S2). Interestingly, a recent report showed that the enhanced adaptability to salt stress of the *Panicum miliaceum* L. genotype appeared to originate from its ability to shape its rhizospheric microbial community, which included *Acremonium* (Yuan et al., 2023). That could indicate a more universal role of *Acremonium* in promoting salt tolerance.

4.2 | Putative mechanisms promoting growth in response to *Acremonium* under salt stress

To elucidate the molecular mechanisms underlying salinity stress alleviation by *Acremonium*, aerial parts of *B. napus* plants were subjected to different omics analyses (Figure 4A-C; Tables S1, S2). While analyzing roots would be optimal, simulating a natural environment necessitated growing seedlings in Jiffy pots. Unfortunately, the resulting entwined and fragile root systems within the substrate hindered unbiased omics analyses. Nevertheless, the analysis of the collected shoots pointed to several mechanisms that could explain the promoted growth under salt stress conditions. Comparing dry and fresh weights revealed no significant difference in relative water content between *Acremonium*-inoculated and mock-inoculated plants under salt stress. This contradicts one of the putative mechanisms whereby the fungus promotes water uptake in plants. A recent study suggested that upregulating genes for chlorophyll a/b binding proteins might enhance salt tolerance in *Brassica napus* (Xue et al. 2024). Supporting this hypothesis, *Acremonium* inoculation under salt stress significantly increased the abundance of over 20 photosynthetic proteins, including various chlorophyll a/b binding proteins, Cytochrome b559 subunits, the PS II D2 protein, photosystem I apoproteins A, and both PS I and PS II reaction center subunits. Additionally, a statistically significant ($p < 0.05$) but modest increase was observed in an ortholog of Protein HIGH CHLOROPHYLL FLUORESCENCE PHENOTYPE 244, known to be involved in PS II biogenesis (Table S2). These results collectively suggest an increase in photosynthetic activity. These observations are further corroborated by chlorophyll fluorescence measurements in *Arabidopsis* (Figure S2), including the significant increase in the chlorophyll fluorescence decrease ratio (R_{Fd}) that directly correlates with the net CO_2 assimilation rate (Lichtenthaler et al., 2005). However, the present data cannot rule out the alternative explanation that the observed increase in these proteins in *Acremonium*-treated plants under salt stress is a consequence of enhanced growth rather than a causative factor.

Among the DAPs identified as potentially contributing to *Acremonium*-mediated salt tolerance, the second most abundant category consists of 13 ribosomal proteins alongside a distinct set of translation-related proteins. Notably, despite the relatively small number of identified ribosomal proteins compared to the hundreds of genes encoding them in plants, these DAPs collectively represent nearly 10% of the estimated total ribosomal protein abundance in *Brassica napus* plants (Table S2). Previous experiments demonstrated contrasting translational dynamics and ribosome stalling in the salt-sensitive rice genotype (Yang et al. 2021) and that a mutant in plastidic ribosomal protein was more tolerant to salt in *Arabidopsis*

(Xu et al. 2013). These findings suggest that *Acremonium*'s influence on salt tolerance might involve modulations in ribosomal composition. Notably, while ribosomal proteins were also identified in *Acremonium*'s response under control conditions, these did not overlap with the set of DAPs observed under salt stress (Table S2).

While several phytohormones are well-known orchestrators of growth responses to environmental stimuli, abscisic acid appears to have the leading role in promoting salt tolerance in *Acremonium*-inoculated plants (Figure 5A-D). The observed increase in enzymes of the isoprenoid metabolic pathway, namely 4-hydroxy-3-methylbut-2-en-1-yl diphosphate synthase and 4-diphosphocytidyl-2-C-methyl-D-erythritol kinase (both with increases exceeding 1.5-fold; adjusted $p < 0.05$), likely reflects an upregulation in its biosynthesis. However, other potential players emerged among the set of candidate proteins. These included orthologs of the jasmonate-responsive Cystine lyase CORI3 (3-fold increase in abundance, adjusted $p < 0.05$), jasmonate metabolism enzymes 12-oxophytodienoate reductase (3-fold increase, adjusted $p < 0.05$) and Lipoxygenase 2 (dominant isoform XP_013648532.1; a significant decrease in abundance only in mock-treated plants under salt stress), and Nitrilase 2 (1.3-fold increase in abundance, adjusted $p < 0.05$), capable of converting indole-3-acetonitrile to the plant hormone auxin. Intriguingly, despite these protein changes, no corresponding alterations were observed in the pool of jasmonic acid (levels below the detection limit) or auxin (no significant differences; Table S1).

Our analysis identified additional candidate proteins with established roles in abiotic stress responses, including orthologs of a phytocyanin Early nodulin-like, mitochondrial NAD-dependent malic enzyme and fucosidase (1.4–1.6-fold increase, adjusted $p < 0.05$; Table S2). Phytocyanins have been shown to promote salt stress tolerance in some plant species (Cao et al. 2015; Wang et al. 2019). Malic enzyme contributes to maintaining TCA, amino acid, and carbohydrate metabolism. Fucose accumulation might be part of the regulatory network during salt stress (Jiao et al. 2022), and increased fucosidase abundance coincided with a small but significant rise in fucose levels in inoculated plants under salt stress (1.2-fold increase, adjusted $p < 0.05$; Table S1). Increased ferritin abundance (Ferritin 1 and two isoforms of Ferritin 3; 1.4–2.4-fold increase, adjusted $p < 0.05$; Table S2) could also contribute, as shown by transgenic *Arabidopsis* expressing wheat *Ferritin5D* with improved tolerance to drought and salt (Zhang et al. 2023). Finally, changes in free amino acids, including tryptophan (1.4-fold increase, adjusted $p < 0.05$; Table S1), have also been linked to microbe-mediated salt tolerance (Annadurai et al. 2021).

4.3 | *A. alternatum* enhanced antioxidant system and ion sequestration via an interplay between abscisic acid and ROS

The inoculation with *Acremonium* correlated with the accumulation of several phenolic compounds, including trans-ferulic and cis-caffeic acids. Notably, these compounds were also induced by salt stress, but inoculated plants exhibited significantly higher levels (1.3–1.6-fold increase in abundance, adjusted $p < 0.05$; Table S1). The increased phenolic content aligns with previous reports and with their importance in ROS scavenging for stressed plants (Chen et al. 2019; Jan et al. 2022). This potential role is further supported by similar, albeit statistically inconclusive, increases in several other salt-responsive secondary metabolites known for ROS scavenging in inoculated plants under salt stress. Notably, pantothenic acid (1.2-fold increase), previously linked to improved salt tolerance (Yonamine et al. 2004), falls within this category. Taken together with the observed changes in abundances of ROS metabolic enzymes (Table S2) and ROS levels (hydrogen peroxide and superoxide radical; Figure 6A-D), it seems that there is a substantial role for ROS modulation in *Acremonium*-mediated growth promotion under salt stress. A recent study showed that abscisic acid priming promotes salt tolerance in maize seedlings by modulating ROS homeostasis (Sarkar et al. 2023). The connection is not surprising given the conserved abscisic acid-responsive elements (ABRE) generally found in promoters of ROS metabolism enzymes (Dufková et al. 2019; Su et al. 2021). Apart from these, *Acremonium*-primed plants accumulated other proteins potentially linked to abscisic acid responses and signaling, such as GDSL-type Esterase/Lipases (three isoforms, 1.6–24.0-fold increase in abundance; Table S2), known to interact with phytohormones and respond to different abiotic factors (drought, salt stress) through *cis*-acting elements in their promoter regions (Su et al. 2020; Duan et al. 2023), a Ca^{2+} sensing receptor (1.4-fold increase, adjusted $p < 0.05$) potentially facilitating calcium release from chloroplasts (Han et al. 2003; Nomura et al. 2008), and multiple V-ATPase subunits, well-established abscisic acid targets (Barkla et al. 1999).

Plants achieve salt tolerance by adapting their ion transport networks to regulate ion homeostasis, retaining essential ions and decreasing harmful ones (Flowers et al. 2015). While endophytic fungus *Serendipita indica* inoculation upregulates genes encoding ion channels for Na^+ and K^+ (Abdelaziz et al. 2017), *Acremonium*-inoculated plants did not show significant changes in corresponding genes. However, as described in results, they exhibited a striking increase in V-ATPase abundance, an essential complex facilitating ion sequestration in the apoplast or vacuole (Zhu 2001). Interestingly, a recent study showed that *Streptomyces* promotes plant growth under salt stress by upregulating *V-ATPase* genes in rice (Kruasuwan et al. 2023), suggesting a similar mechanism employed by *Acremonium*-inoculated plants under salt stress.

5 | CONCLUSIONS

B. napus, a widely cultivated oilseed crop spanning roughly 35 million hectares worldwide (Faostat, 2022), faces various stress factors, including salt stress, which reduces plant height, size, and yield (Naheed et al. 2021; Shahzad et al. 2022). Endophytic microorganisms are known to promote plant growth and biomass production (Azad and Kaminskyj 2016; Rho et al. 2018; Zhang et al. 2019). In this study, inoculation with the endophyte *Acremonium alternatum* increased

both fresh and dry weight under salt stress conditions. Further molecular analyses provided insights into the potential mechanisms involved, highlighting a putative role of abscisic acid in mediating ROS metabolism and ion sequestering. These findings contribute to our understanding of plant-fungi interactions and offer promising leads for developing novel biological agents to improve crop production under the challenges posed by climate change.

AUTHOR CONTRIBUTIONS

VB, MB, and MČ initiated the study. VB designed the experiments. VB, LŠ, and SM conducted physiological studies. JĎ and JK performed microscopy. VB, MB, LŠ, and MČ performed proteomics and metabolomics studies. SK provided anion analyses. VB, MB, JK, and MČ prepared figures. SA, BB, SK, and JLM contributed to data analysis and interpretation. VB, MB, and MČ wrote the manuscript. MČ finalized the manuscript. All authors approved the published version.

ACKNOWLEDGEMENT

Open access publishing facilitated by Mendelova univerzita v Brne, as part of the Wiley - CzechELib agreement.

FUNDING INFORMATION

This work was supported by the Czech-German mobility projects 8J23DE004 and 7AMB18DE015, MSTC Danube project n. 8X23011, and the Internal Grant Schemes of Mendel University in Brno. Reg. no. CZ.02.2.69/0.0/0.0/19_073/0016670. SK research is funded by the DFG under Germany's Excellence Strategy – EXC 2048/1 – project 390686111.

DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are available within the paper and within its supplementary data published online, via the PRIDE partner repository (http://proteomecentral.proteomexchange.org) with the dataset identifiers PXD049437.

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How to cite this article: Berková, V., Berka, M., Štěpánková, L., Kováč, J., Auer, S., Menšíková, S. et al. (2024) The fungus *Acremonium alternatum* enhances salt stress tolerance by regulating host redox homeostasis and phytohormone signaling. *Physiologia Plantarum*, 176(3), e14328. Available from: https://doi.org/10.1111/ppl.14328