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RESEARCH

Enhancing Weed Suppression in Plants by Artificial Stress Induction

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Abstract

Various plant species from the Poaceae, Cannabaceae, and Brassicaceae families are used as cover crops to suppress weeds and volunteer crops through competition and allelopathy. This study examined the effects of artificially induced stress on the physiological processes, total phenolic content (TPC), and allelopathic potential of the plant species *Avena strigosa, Cannabis sativa*, and *Sinapis alba* at an early growth stage with the aim to increase their weed suppression abilities. Stress was induced at the 3–4 leaf stage in greenhouse-grown plants via harrowing, methyl jasmonate (MeJA) application, insect stress simulation, or a combination of insect stress and harrowing. Maximum quantum yield of photosystem II and shoot dry matter in the three plant species were only minimally or not affected a few days after treatment (DAT). Insect stress caused visible symptoms on treated leaves in all plants. The TPC in the shoot extracts of combined stress-treated *C. sativa* and insect-stressed *S. alba* was significantly higher by 1.7 and 1.9 times, respectively, five DAT compared to the shoot extracts from untreated control plants. Additionally, laboratory bioassays with aqueous shoot extracts from the untreated and treated plants were conducted to identify changes in allelopathic potential within the shoot tissues. The application of shoot extracts from MeJA-treated *C. sativa* and *S. alba* resulted in the lowest seed germination rates for the two weed species *Alopecurus myosuroides* and *Stellaria media*, as well as for the volunteer wheat *Triticum aestivum*, which were up to 65% lower 10 DAT compared to seeds treated with shoot extracts from non-stressed plants. However, the root-suppressing effect of the shoot extracts on weeds was not influenced by the stress treatments. This study reveals that artificial stress induction can be a suitable management strategy to enhance weed and volunteer cereal suppression in plants in an early growth stage but may vary between stress types and plant species, and requires further optimization and field testing.

Keywords Allelopathy · Artificial stress induction · Cover crops · Hermetia illucens · Phenolic accumulation · Phytohormone application

Introduction

The Farm to Fork and Biodiversity Strategy, proposed by the European Commission under the European Green Deal, targets to reduce the use of synthetic pesticides on EU agricultural lands by half until 2030 (European Commission 2020). This underscores the growing importance of utilizing alternative and efficient methods in integrated pest management to effectively control weeds, pests, and diseases. Consequently, researchers are exploring innovative preventive management strategies based on biological and physical approaches. The implementation of cover crops (CCs) between consecutive main crops, as part of an integrated management strategy, has the potential to control weeds and volunteer cereals in the field by inhibiting their shoot and root growth, as well as their germination (Brust et al. 2014; Schappert et al. 2019). Studies have shown that CCs can reduce weed and volunteer biomass by up to 95% in temperate zones when growing during the period following the late summer/fall harvest of the main crop until the spring sowing of the subsequent main crop (Gerhards and Schappert 2019). In addition to their weed-suppressive properties, CCs can prevent soil from erosion by wind or water (De Baets et al. 2011) and absorb nitrates and other nutrients mainly from the upper soil layers, followed by their recycling and redistribution (Hooker et al. 2008;

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Blanco-Canqui et al. 2012). Furthermore, CCs possess the ability to improve soil structure, promote the accumulation of organic matter (Hartwig and Hoffman 1975), improve hydraulic properties (Haruna et al. 2018), and play a major role in fostering biodiversity by acting as an extra food source and offering habitats for beneficial pollinators, mammals, insects, and microorganisms (Tillman et al. 2004). Weed suppression by CCs in general results from a combination of two main effects:

1. Resource competition for nutrients, light, space and water (Sturm et al. 2018).
2. Allelopathy mediated by allelochemicals released from living (Jabran et al. 2015) and/or decomposing cover crop (CC) tissues (Sturm et al. 2016)

In ecosystems, phenolic compounds are some of the key and most widely distributed plant allelochemicals (Li et al. 2010). Phenolic compounds are metabolized in plants via the shikimic and acetic acid pathways (Li et al. 2010). They are associated with several plant physiological functions such as the germination, the mitosis, and the biosynthesis of photosynthetic pigments (Tanase et al. 2019). Furthermore, they have a central function in the plant's defence mechanisms against abiotic and biotic stressors (Tuladhar et al. 2021). Water-soluble allelochemicals such as phenolic compounds significantly influencing the allelopathic potential of CCs with both concentration-dependent stimulatory or inhibitory effects on neighbouring plants (Batish et al. 2002; Đorđević et al. 2019). Furthermore, beside the phenolic compounds, there are several other known phytotoxic secondary metabolites that can vary greatly between plant families. Asteraceae species, for example, mainly contain sesquiterpenes, triterpenes and flavonoids (Macías et al. 2006), whereas Poaceae species primarily contain benzoxazinoids and benzoquinones (Stochmal et al. 2006, Baerson et al. 2008). In contrast, the main allelochemicals identified in Brassicaceae species are glucosinolates with their hydrolysed products and brassinosteroids (Rehman et al. 2018), whereas in Cannabaceae species the allelopathic effect assumed to originate mainly from phytocannabinoids, terpenes and phenols (Patanè et al. 2023; Shikanai and Gage 2022).

Allelochemical contents in plants vary due to several factors such as plant responses to abiotic and biotic stresses, plant growth stage, plant age and variety of the plant species (Belz 2007). Abiotic stresses encompass a range of factors, including temperature (heat, cold, freezing), water availability (drought, flooding), chemicals (salinity, inadequate pH, ozone, phytohormones, plant activators, pesticides, nutrient deficiencies/excess, heavy metal excess), radiation (UV-A, UV-B, infrared, ionizing, photoinhibition, photooxidation), and other influences (mechanical wounding, wind, magnetic fields) (Belz 2007; Weston and Duke 2003; Kruidhof et al. 2014; Bi et al. 2007). Biotic stress affecting plants secondary metabolite levels is induced by neighbouring plants, herbivores, and pathogens (Maqbool et al. 2013; Foyer et al. 2016). Several studies with Brassicaceae species have shown that artificially induced stresses, such as mechanical stress through harrowing (Kruidhof et al. 2014), insect stress through simulated insect attacks (Bodnaryk 1992), and phytohormonal stress through the application of the phytohormone methyl jasmonate (MeJA) (Baenas et al. 2014), can increase glucosinolate production. Additionally, Kong et al. (2006) showed that the content of phenolic compounds in soil increases when *Oryza sativa* L. seedlings (3-leaf stage) are grown in the presence of the weed *Echinochloa crus-galli* L.. Therefore, phenolic compounds are useful indicators for the general allelopathic activity of plants. Nevertheless, the impact of stress induction on the production of phenolic compounds of plant species belonging to Brassicaceae, Cannabaceae, and Poaceae species remains underexplored. *Avena strigosa* Schreb., *Cannabis sativa* L., and *Sinapis alba* L., as representatives of these plant families, are known for their notable allelopathic properties (Rueda-Ayala et al. 2015; Sturm et al. 2016) and can be used as CCs. These species are well adapted to dry, warm climates, are very competitive due to their fast growth and canopy closure, and can significantly reduce weed pressure, making them suitable for cover cropping in temperate zones (Schappert et al. 2019; Rueda Ayala et al. 2015; Brust et al. 2014; Ranalli 1999).

The objectives of this study were to provide initial insights into the impact of three different artificially applied stresses and a stress combination on key physiological processes in the three plant species *A. strigosa, C. sativa*, and *S. alba* during their early growth stage. Furthermore, the impact of these stresses on the phenolic compound content of aqueous *A. strigosa, C. sativa*, and *S. alba* shoot extracts, and on their allelopathic potential on the two annual weed species *Alopecurus myosuroides* Huds. and *Stellaria media* L., as well as the cereal crop species *Triticum aestivum* L., which can occur as volunteer crop after cereal harvest, were investigated in laboratory bioassays. In detail, the following hypotheses were tested:

3. (i) Stress induction in the test plants leads to minimal losses in shoot biomass and minimal reductions in the maximum quantum yield of photosystem II.
4. (ii) Plants exhibit defense reactions after stress induction via applied paste of dead adult *Hermetia illucens* L..
5. (iii) Stress treatments increase the total phenolic content in aqueous shoot extracts produced from stress-treated *A. strigosa, C. sativa*, and *S. alba*, thereby enhancing the allelopathic effects of these extracts on *A. myosuroides, S. media*, and *T. aestivum*.

6. (iv) *T. aestivum* is less affected by aqueous shoot extracts compared to the weed species *A. myosuroides* and *S. media*.

Material and Methods

Plant Material, Used Stressors and Experimental Design

Greenhouse trials were carried out twice at two separate time intervals (2021 and 2022) at the University of Hohenheim in Stuttgart, Germany. For the plant cultivation, plastic pots (12 cm × 12 cm × 13 cm) were filled with a soil mixture composed of 50% humus, 25% loam, and 25% sand. The three plant species were sown at their recommended field rates: *A. strigosa* L. var. Panache (80 kg ha^{-1}, thousand kernel weight (TKW): 21 g); *C. sativa* L. var. Futura 75 (25 kg ha^{-1}, TKW: 8 g), and *S. alba* var. Litember (20 kg ha^{-1}, TKW: 6 g). Therefore, plant density for each plant species was 5 plants per pot. Day/night temperatures in the greenhouse were maintained at 20 °C/15 °C. In addition to daylight, a sodium vapor lamp (400 W, 37,500 lm) was used for 12 h per day. The plants were irrigated with water every day and no fertilizers were applied in the trials. Stress was applied during the critical growth phase, specifically at the three to four leaf stage (BBCH 13–14). The experimental stress treatments comprised:

1. *Untreated control.* Plants were cultivated without any stress treatment.
2. *Mechanical stress treatment.* The pots were manually traversed by hand with a harrow equipped with flexible metal tines (Ø 8 mm) at a soil depth of 4 cm and a speed of 4 km/h.
3. *Phytohormonal stress treatment.* The phytohormone MeJA was applicated at a concentration of 0.5 mg MeJA per ml deionized water (dH_2O) (total formulation: 50 ml) using an automatic spray chamber (Schachtner, Ludwigsburg, Germany). The spray chamber was adjusted to a calibration of 200 L ha^{-1}, operating at a speed of 788 mm s^{-1} and a pressure of 3.6 bar. The application involved the use of a nozzle with a spray rate of 0.8 L/min and was positioned 90 cm above the plant canopy.
4. *Insect stress treatment.* Dead adult *H. illucens* (Madebymade GmbH, Pegau, Sachsen, Germany) were homogenized with dH_2O using a mixer to create the stock paste. Thereby, the concentration of the stock paste was 2 g of dead adult *H. illucens* per ml dH_2O. To simulate insect-induced frass damage, a circular hole with a diameter of 5 mm was manually punched into each of the two oldest true leaves, employing a leather puncher. Due to the elongated and thin leaf morphology of *A. strigosa*, it was not feasible to punch holes. Instead, the leaf tip (the uppermost 2 cm of the two oldest true leaves) was excised using a scissor. Subsequently, each plant was subjected to a treatment involving the application of 0.4 g of homogenized adult *H. illucens* paste, which was carefully applied around the two punched holes or the cut edges of the leaves using a brush. *H. illucens* were used for the insect paste because they can be produced commercially in large quantities and therefore are available in sufficient quantities for future field applications.
5. *Combination of mechanical and insect stress.* First harrowing (see mechanical stress treatment) followed by an application of dead adult *H. illucens* after leaf injuries (see insect stress treatment).

A randomized complete block design consisting of four blocks (one block ≙ one repetition) and two factors were chosen for the experimental design in the greenhouse trials. The first factor comprised the ‘stress treatments’, while the second factor the ‘plant species’. For the chlorophyll fluorescence measurements, however, the factor ‘Day’ was used as the second factor. Each block consisted of one replicate of each treatment, including untreated plants serving as controls.

Data Collection in the Greenhouse Experiments

Chlorophyll fluorescence analysis. The utilization of chlorophyll fluorescence imaging technology offers a significant advantage by enabling non-destructive assessment of PS II physiological response in plants, particularly during initial phases, given its high sensitivity to detecting abiotic and biotic stress (Li et al. 2017). The chlorophyll fluorescence measurements were conducted immediately prior to stress application (zero days after treatment), as well as at intervals of two and four days after the application of the stress treatments. Early measurement intervals were used because preliminary tests and other studies (Quan et al. 2023; Commault et al. 2021) have shown that changes in the maximum quantum yield of photosystem II (PS II) in the plants can occur within few days after stress treatment. Pots were dark-adapted for 30 min before the measurement using plastic lids. The maximum quantum yield of the PS II was measured as described by Li et al. (2017) with a fluorescence sensor (IMAGING-PAM®, Heinz Walz GmbH, Eiffeltrich, Germany). The maximum quantum yield of PS II (F_v/F_m) is a ratio formed by F_v and F_m. F_m representing the maximum fluorescence yield and F_0 the minimum fluorescence yield. F_v is the maximum fluorescence yield (F_m) minus the minimum fluorescence yield (F_0).

$$F_v/F_m = \frac{(F_m - F_0)}{F_m}$$

Biomass Sampling and Shoot Dry Matter Determination To determine dry matter and produce aqueous shoot extracts for Petri dish bioassays and chemical analysis, the shoot biomass of untreated and treated plants was harvested five days after stress application. The shoot biomass used for the preparation of the aqueous shoot extracts was stored at –20 °C in a freezer for two weeks until further processing. The shoot biomass collected for the shoot dry matter determination was placed in paper bags and subjected to a drying process at 80 °C for a duration of three days. Thereafter, the shoot dry matter was weighed to the nearest two decimal places (g), and the total weight per pot was extrapolated to represent the weight of an individual plant.

Laboratory Petri Dish Bioassays with Aqueous Shoot Extracts

Petri dish bioassays with aqueous shoot extracts made from the stressed and non-stressed greenhouse-grown plant species (Sect. "Data collection in the laboratory Petri-dish bioassay") were carried out twice at two separate time intervals (2021 and 2022) in the laboratory to evaluate the impact of the stress treatments on their allelopathic potential on weeds and volunteer cereal. Therefore, the aqueous shoot extracts were applied on the monocotyledonous weed species, *A. myosuroides*, the dicotyledonous weed species *S. media*, and on the cereal crop *T. aestivum*. Both weed species are prevalent in cereal fields and capable of causing substantial yield losses if uncontrolled (Zeller et al. 2021; Kauppi et al. 2021). Additionally, *T. aestivum* can become a problem as a volunteer crop after cereal harvest. Similar to greenhouse trials, the experimental design comprised a randomized complete block design consisting of four blocks (four repetitions) and two factors. The first factor encompassed the stress treatments, while the second factor involved the plant species. Each block in the Petri dish bioassays included two controls and each stress treatment. The untreated control involved the application of 3 ml of aqueous shoot extracts from non-stressed plant species, while the aqueous control consisted of the application of 3 ml of deionized water only.

Aqueous shoot extracts were prepared according to Rueda-Ayala et al. (2015) and Sturm et al. (2016). We chose a higher concentrated stock solution for the shoot extracts than the mentioned authors to identify differences between the different stress treatments more easily and to minimize the possibility of hormetic effects. Preliminary tests have also shown that the phytotoxicity of the aqueous shoot extracts increases with increasing biomass concentration in most investigated plant species. The harvested frozen shoot biomass was finely chopped and pulverized using liquid nitrogen. For each of the two experimental trials, 50 ml crude shoot extracts were prepared per plant species and treatment (including untreated control) at a ratio of 1 ml DH_2O per 0.5 g frozen shoot biomass. The crude shoot extracts were subjected to agitation on a laboratory shaker for 24 h at 400 rpm, followed by centrifugation at room temperature (4400 rpm, 10 min). Following centrifugation, the supernatant was carefully decanted using a pipette and subsequently filtered under vacuum through a Büchner funnel containing a filter paper (Ø 60 mm, Cytiva Whatman, Marlborough, USA). The resulting filtrate served as the stock solution with a concentration of 0.5 g ml^{-1}. For the bioassays, 20 seeds of *A. myosuroides* and *S. media* (Appels Wilde Samen GmbH, Darmstadt, Germany), along with 10 seeds of *T. aestivum*, were evenly distributed on filter paper placed in Petri dishes (Ø 60 mm, Cytiva Whatman, Marlborough, USA). Subsequently, 3 ml of the corresponding stock solution was applicated. Petri dishes, which had been previously sealed with Parafilm® M (Bemis Company, Wisconsin, USA), were randomly distributed in the respective block within the climate chamber (Model KBF 720, Binder GmbH, Tuttlingen, Germany). The temperature conditions were set at 20 °C (day) and 15 °C (night), while a simulated photoperiod of 12 h of light, providing an illumination intensity of 14,000 lx, and 12 h of darkness was maintained.

Data Collection in the Laboratory Petri-dish Bioassay

After a period of 10 days, the root length (mm) and the germination rate (%) were assessed using graph paper. In this context, only roots with a length of ≥ 2 mm were measured, while seeds with a root length < 2 mm were classified as non-germinated. The germination rate was determined using the following formula (Scott et al. 1984):

$$GR = \frac{n}{N} x100$$

Where n equals the number of germinated seeds and N is the number of seeds per treatment.

Chemical Analysis of the Aqueous Shoot Extracts

Total Phenolic Content (TPC) Measurement of Aqueous Shoot Extracts

The Folin-Ciocalteau-Micro method (Slinkard and Singleton 1977; Narlı et al. 2006) was used for the determination of the TPC of the different prepared aqueous shoot extracts as shown in Sect. “Laboratory Petri dish bioassays with aqueous shoot extracts”. Each prepared aqueous shoot extract was measured. A gallic acid stock solution (0.5 g dry gallic acid in 10 ml ethanol) and a sodium carbonate solution (200 g anhydrous carbonate in 800 ml autoclaved water) were firstly produced. Then aliquots (20 µl of each shoot extract) were mixed with 1.58 ml water (autoclaved) and 100 µl Folin-Ciocalteau reagent (Sigma-Aldrich, Steinheim, Germany). After eight minutes at room temperature, 300 µl sodium carbonate solution was added. After another incubation of 35 min at 37 °C, a spectrophotometer (PM6, Analysen Technik Graete, Germany) with an adjusted wavelength of 760 nm was used to determine the absorbance of the prepared solutions. For the expression of the results the measurement unit mg gallic acid equivalent (GAE) g^{-1} extract-fresh weight (shoot biomass of the investigated plant species) was selected. Subsequently, the measured values were compared with the prepared gallic acid calibration curve (0, 50, 100, 150, 200, 300, 400 µg mL^{-1}) ($R^2 = 0.9858$).

GC-MS/MS Analysis of Aqueous Shoot Extracts

In preparation for the chemical analysis of the aqueous shoot extracts using a gas chromatography (GC-FID: Agilent 7890B, Agilent Technologies, Waldbronn, Germany) with an integrated flame ionization detector connected to an Agilent 7000D triple quadrupole mass spectrometer (Agilent Corp., Waldbronn, Germany), the samples were first centrifuged (4400 rpm, 10 min) before 200 µL were taken from each sample. The aliquots were then dried at 45 °C using a SpeedVac (Thermo Electron, Dreieich, Germany), derivatized with 50 µL pyridine and 100 µL N,O-bis(trimethylsilyl)trifluoroacetamide at 60 °C for 45 min at 350 rpm and finally 1 µL was injected into the GC (pulsed splitless injection mode). The GC had the following settings: Helium (carrier gas) with a flow rate of 1 ml min^{-1}, at an injection temperature of 250 °C. The GC temperature program was started at 80 °C for 2 min, then heated to 320 °C at a rate of 5 °C min^{-1} and held for 2 min. The transfer line was at 250 °C. All produced aqueous shoot extracts from all treatments including the controls (untreated plants) were measured. The chemical substances found in the samples were compared with phenolic compounds from the standard reference database NIST 17 (National Institute of Standards and Technology, Gaithersburg, USA) for identification, and the respective peak areas were calculated. The mean peak areas of the respective phenolic compounds detected in the aqueous shoot extracts of the untreated control plants (MAP_C) were then compared with those detected in the aqueous shoot extracts of the treated plants (MAP_T). The following formula was utilized to calculate the treatment effect (TE) as a percentage:

$$TE = \left(\frac{MAP_T}{(MAP_C/100)}\right) - 100$$

Statistical Analysis

Greenhouse Trials, Laboratory Petri Dish Bioassays and Total Phenolic Content Data Data analysis was conducted using the statistical software R Studio (Version 2023.06.2+561.pro5., RStudio Team, Boston, MA, USA), and graphs were generated with Origin (Pro) Version 2023 (OriginLab Corporation, Northhampton, MA, USA). A two-way analysis of variance (ANOVA) was used to determine statistical differences ($p < 0.05$). The RStudio package ‘emmeans’ was chosen for the post-hoc test, performing a tukey-adjusted pairwise comparison of the mean values. The analysis employed a two-factor linear mixed model with the two factors ‘stress treatment’ and ‘plant species’.

Q-q plots and the Levene’s Test were used to test the variance homogeneity of the data, whereas the Shapiro-Wilk test was employed to assess normal distribution. When required, the transformation of the data was done, using the log transformation or square root to meet the assumptions for the ANOVA analysis.

Phenolic Compounds Data from GC-MS/MS Analyses A one-way ANOVA with the factor ‘stress treatment’ was used for the statistical analysis of the area peaks of the single phenolic compounds. Comparisons were made between the different stress treatments, including the untreated control plants, whereby the different phenolic compounds and the three plant species were investigated separately. Further steps of the statistical analysis did not differ from the procedures described above.

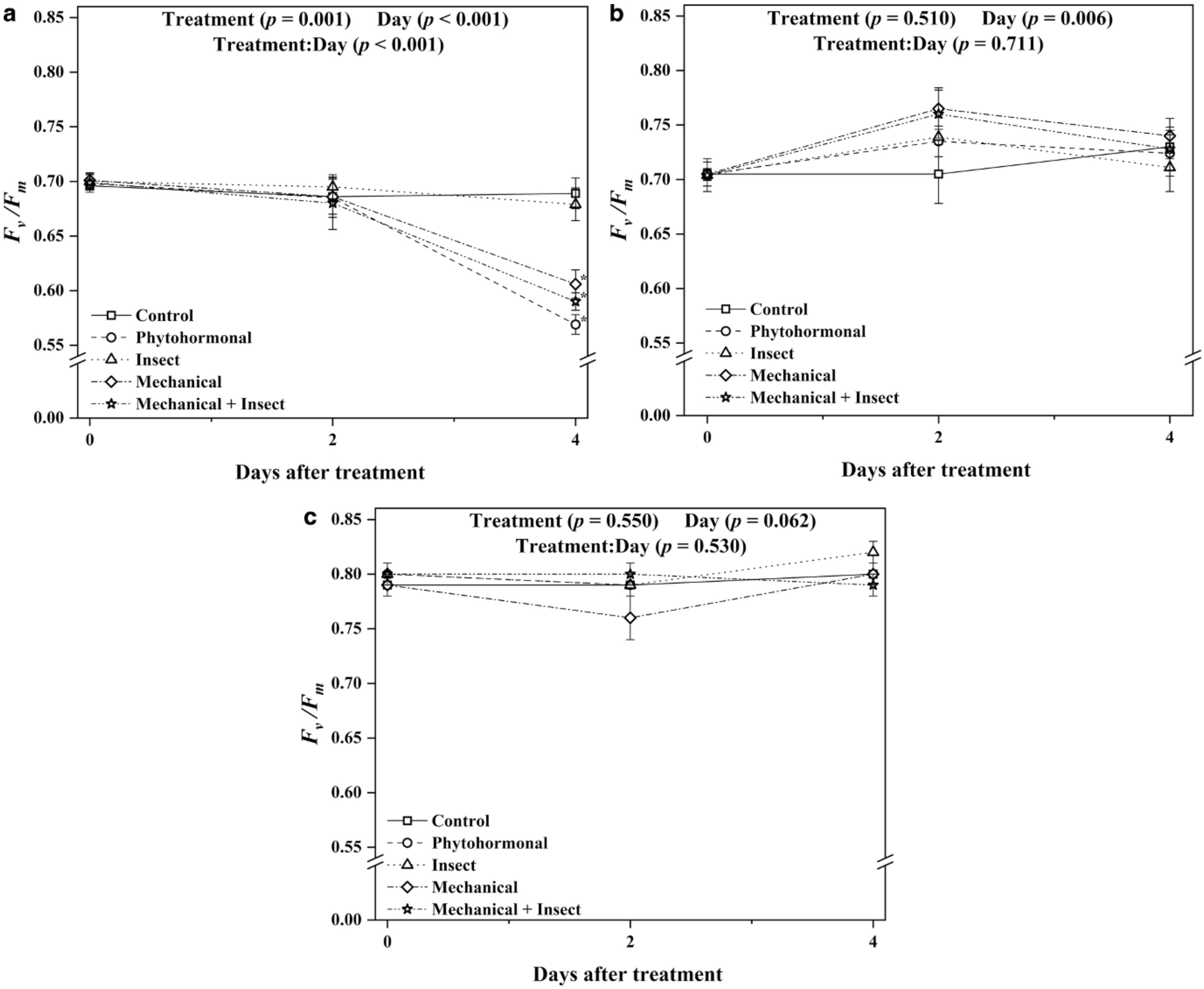

Fig. 1 Means of the maximum quantum yield of photosystem II (F_v/F_m) of untreated and treated *Avena strigosa* (A), *Cannabis sativa* (B), and *Sinapis alba* (C), with standard deviations (SD) at zero days, two days, and four days after the artificial stress induction. Asterisks (*) denote significant differences from the control on the same day for the respective stress variants according to the post hoc test ($p < 0.05$). The *p*-values for the first factor 'Treatment', the second factor 'Day', and their interaction are shown. Treatments: Control = untreated plants; phytohormonal = methyl jasmonate application; insect = *Hermetia illucens* paste application + mechanical leaf injury of the two oldest true leaves; mechanical = harrowing; mechanical + insect = harrowing + *Hermetia illucens* application

Results

Influence of Stress Factors On the Maximum Quantum Yield of the Photosystem II of Avena Strigosa*,* Cannabis Sativa *and* Sinapis Alba

Maximum Quantum Yield of the Photosystem II of Avena Strigosa

The two factors 'Treatment' and 'Day' and their interaction showed significant differences ($p < 0.001$) for *A. strigosa*. The application of mechanical stress, phytohormonal stress, and the combined (mechanical + insect) led to a significant decrease in the maximum quantum yield of PSII after four days after treatment (DAT), with reductions between 12 to 17% (Fig. 1a).

Maximum Quantum Yield of the Photosystem II of Cannabis Sativa

Only the factor 'Day' showed significant differences in *C. sativa*. On the second day, the maximum quantum yield of PSII of the plants treated with mechanical stress and the combined (mechanical + insect) stress were significantly higher by 8–9% than the same plants on day 0 (Fig. 1b).

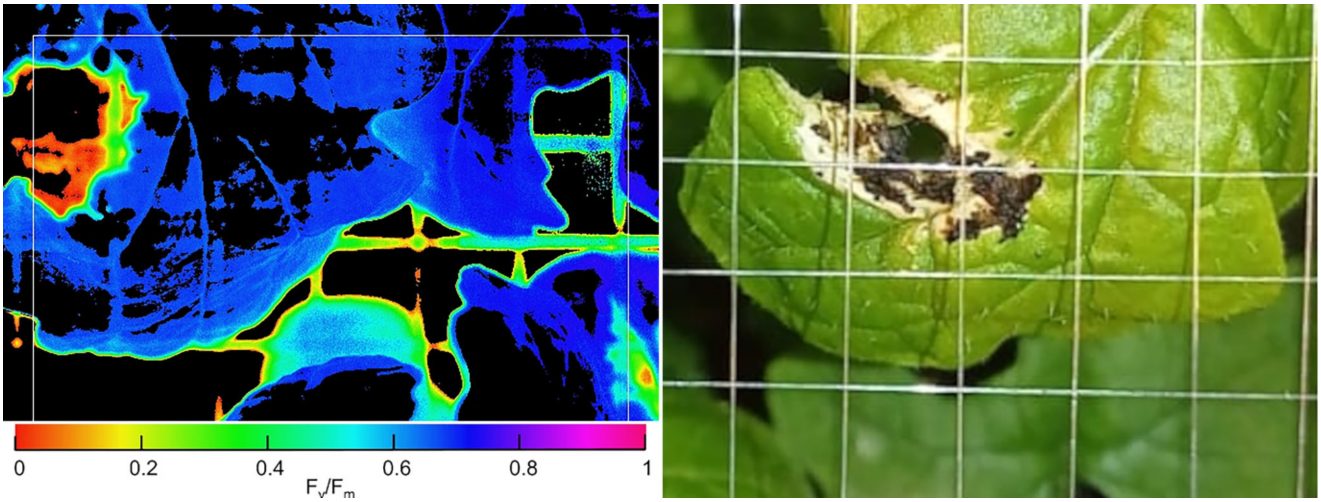

Fig. 2 Chlorophyll fluorescence image displaying maximum quantum yield of the photosystem II represented in false colors (*left*) and the original RGB image (*right*) of *Sinapis alba* two days after the application of insect stress, showcasing visible stress reactions

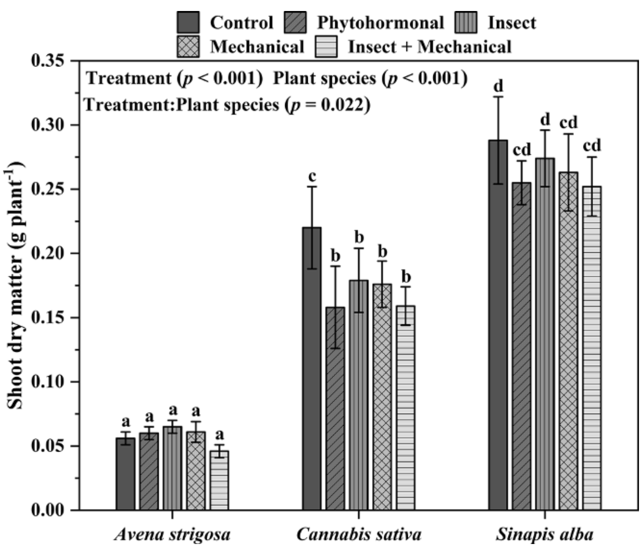

Fig. 3 Shoot dry matter in g per plant of untreated and treated *Avena strigosa*, *Cannabis sativa*, and *Sinapis alba*, with standard deviations (SD) five days after the artificial stress induction. Mean values of shoot dry matter for plants treated with different stressors and controls sharing the same letter were not significantly different from each other according the post-hoc test ($p<0.05$). The *p*-values for the first factor 'Treatment', the second factor 'Plant species', and their interaction are shown. Treatments: Control = untreated plants; phytohormonal = methyl jasmonate application; insect = *Hermetia illucens* paste application + mechanical leaf injury of the two oldest true leaves; mechanical = harrowing; mechanical + insect = harrowing + *Hermetia illucens* application

Maximum Quantum Yield of the Photosystem II of Sinapis Alba

No significant differences in the maximum quantum yield of PSII were measured in *S. alba* across all stress treatments and days compared to the untreated control (Fig. 1c).

Influence of Stress Factors On Plant Leaves Chlorophyll Fluorescence

Of all stress treatments, only the application of the *H. illucens* paste induced a localized visible hypersensitive stress response characterized by necrosis/chlorosis in all three plant species surrounding the injured leaf site as early as 2 DAT. This stress response was confined exclusively to the immediate vicinity of the application area and did not extend beyond that region, as confirmed by chlorophyll fluorescence measurements (Fig. 2).

Influence of Stress Factors On Shoot Dry Matter

The two factors 'Treatment' and 'Plant species' showed significant differences in terms of the shoot dry matter as well as their interaction. In *A. strigosa* and *S. alba*, shoot dry matter was not significantly influenced by any stress treatment. In *C. sativa*, there was a significant reduction in shoot dry matter across all stress treatments, resulting in a significant decrease ranging between 19% (insect stress) and 28% (phytohormonal stress) compared to the untreated control plants (Fig. 3).

Influence of Aqueous Shoot Extracts On Germination Rate and Root Length of Triticum Aestivum

The two factors, 'Treatment' and 'Plant species,' along with their interaction, exhibited significant differences concerning the measured germination rate and root length of *T. aestivum*.

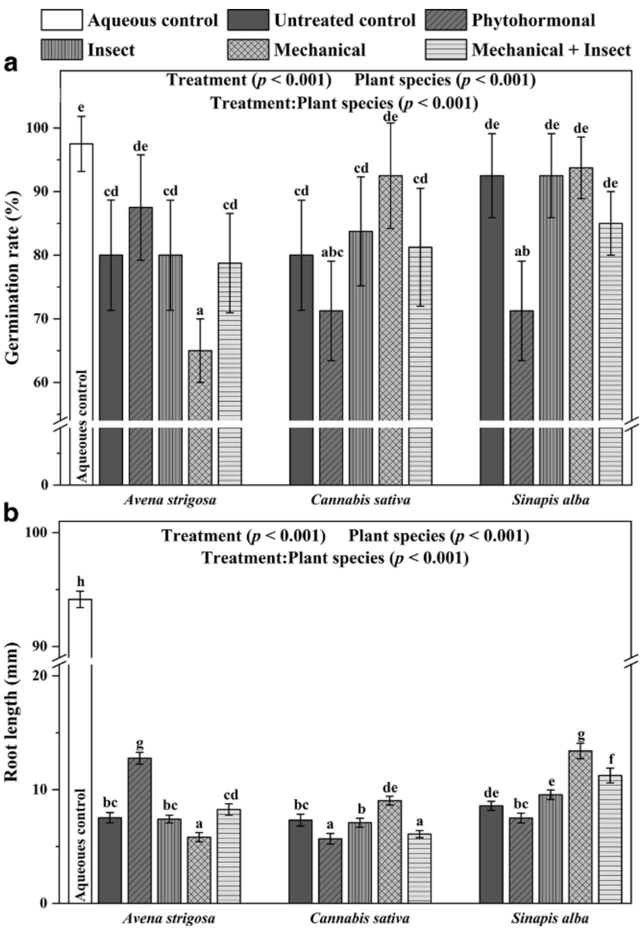

Fig. 4 Mean germination rates (**a**) in % and mean root lengths (**b**) in mm with standard deviations (SD) of *Triticum aestivum* 10 days after the application of aqueous shoot extracts. The shoot extracts were prepared from shoot biomass of stress treated and untreated *Avena strigosa*, *Sinapis alba*, and *Cannabis sativa*. All shoot extracts had a concentration of 500 mg ml^{-1}. Besides the untreated control, the Petri dish bioassay included an aqueous control. Mean values sharing the same letters do not significantly differ according to the post-hoc test ($p < 0.05$). The *p*-values for the first factor 'Treatment', the second factor 'Plant species', and their interaction are shown. Treatments: Aqueous control = deionized water; untreated control = unstressed plants; phytohormonal = methyl jasmonate application; insect = *Hermetia illucens* paste application + mechanical leaf injury of the two oldest true leaves; mechanical = harrowing; mechanical + insect = harrowing + *Hermetia illucens* application

Avena Strigosa *Shoot Extracts*

Compared to the aqueous control, all aqueous shoot extracts (including the untreated control), except for the phytohormonal stress treatment, showed significant reductions in the germination rate of *T. aestivum,* ranging from 18 to 33% (Fig. 4a). All aqueous shoot extracts (including the untreated control) significantly decreased the root length of *T. aestivum* by 86 to 94% (Fig. 4b). Compared to the aqueous shoot extract obtained from the untreated control plants, only the mechanical stress variant significantly reduced the germination rate by 19% and the root length by 23%. In contrast to this, phytohormonal stress resulted in a significantly increased root length by 71%.

Cannabis Sativa *Shoot Extracts*

Relative to the aqueous control, *T. aestivum* showed a significantly decreased germination rate of 14 to 27% due to the application of all aqueous shoot extracts prepared from treated and untreated *C. sativa* plants, except for the mechanical stress treatment (Fig. 4a). Additionally, all aqueous shoot extracts significantly decreased the root length of *T. aestivum* by 90 to 94% (Fig. 4b). Compared to the shoot extract of the untreated control plants, the application of the shoot extracts from mechanically treated plants significantly increased the root length of *T. aestivum* by 23%, whereas the shoot extracts of phytohormonally and combined treated plants led to significant reductions of up to 22%:

Sinapis Alba *Shoot Extracts*

In comparison to the aqueous and untreated controls, a significant reduction in the germination rate of 27 and 23% was observed in *T. aestivum* only when applied with shoot extracts from phytohormonally treated plants (Fig. 4a). However, all aqueous shoot extracts significantly reduced the root length of *T. aestivum* by 86 to 92% compared to the aqueous control (Fig. 4b). The shoot extracts produced from the combined stress (mechanical + insect) and mechanically treated *S. alba* plants significantly increased the root length of *T. aestivum* by 31 and 71% compared to the shoot extracts of the untreated plants, while the shoot extracts from phytohormonally treated plants significantly reduced the root length by 23%.

Influence of Aqueous Shoot Extracts On Germination Rate of the Monocotyledonous Weed Alopecurus Myosuroides and the *Dicotyledonous Weed* Stellaria Media

All investigated shoot extracts reduced the root length of *A. myosuroides* and *S. media* by more than 80% compared to the aqueous control. Since the root lengths did not differ significantly between the stress treatments (including the untreated control plants) and between the plant species, only the results for germination rate are shown for *A. myosuroides* (Fig. 5a) and *S. media* (Fig. 5b). Significant differences in the germination rate of both weed species were observed for the factors 'Treatment' and 'Plant species,' along with their interaction.

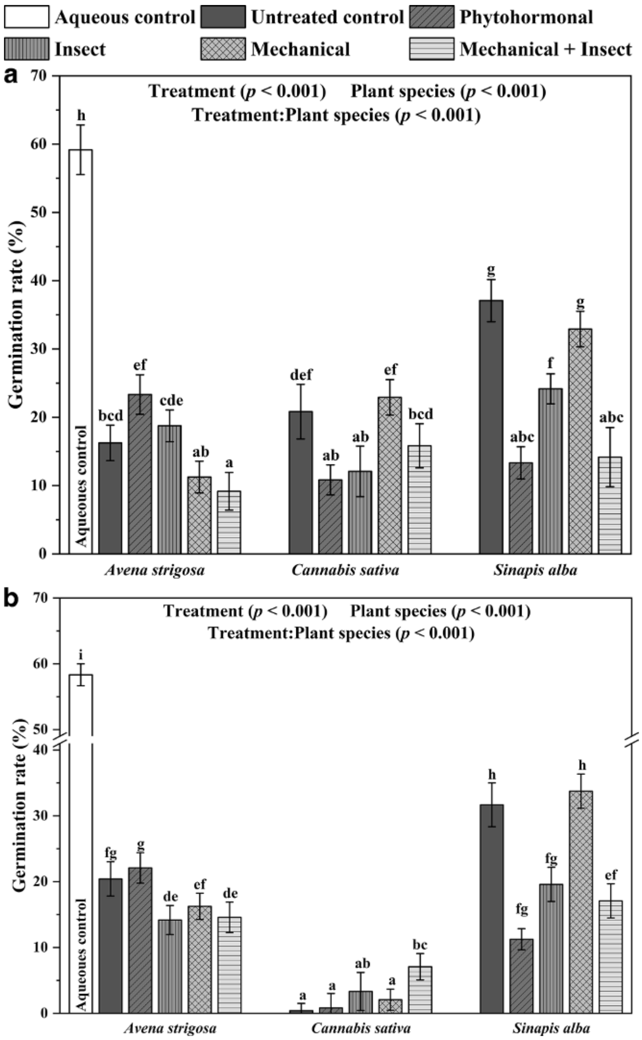

Fig. 5 Mean germination rates in % with standard deviations (SD) of *Alopecurus myosuroides* (**a**) and *Stellaria media* (**b**) 10 days after the application of aqueous shoot extracts. The shoot extracts were prepared from shoot biomass of stress treated and untreated *Avena strigosa*, *Sinapis alba*, and *Cannabis sativa*. All shoot extracts had a concentration of 500 mg ml^{-1}. Besides the untreated control, the Petri dish bioassay included an aqueous control. Mean values sharing the same letters do not significantly differ according to the post-hoc test ($p < 0.05$). The *p*-values for the first factor 'Treatment', the second factor 'Plant species', and their interaction are shown. Treatments: Aqueous control = deionized water; untreated control = unstressed plants; phytohormonal = methyl jasmonate application; insect = *Hermetia illucens* paste application + mechanical leaf injury of the two oldest true leaves; mechanical = harrowing; mechanical + insect = harrowing + *Hermetia illucens* application

Avena Strigosa *Shoot Extracts*

Compared to the aqueous control, all aqueous shoot extracts significantly reduced the germination rate of both weeds by 61 to 85%. Aqueous shoot extracts produced from *A. strigosa* plants treated with insect stress (only in *S. media*) and combined stress (mechanical + insect) resulted in significantly reduced germination rates by up to 40% in both weed species compared to the shoot extracts from untreated control plants. Conversely, the application of shoot extracts from phytohormonally treated plants increased the germination rate of *A. myosuroides* by 43%.

Cannabis Sativa *Shoot Extracts*

Compared to the aqueous control, a significant reduction in the germination rate of both weed species by 61 to 99% was observed by the application of all aqueous *C. sativa* shoot extracts. Relative to the shoot extracts produced from the untreated control plants, the application of shoot extracts produced from MeJA and insect treated *C. sativa* plants showed significant decreases regarding the germination rate of *A. myosuroides* by up to 48%. In contrast, the aqueous shoot extracts obtained from *C. sativa* plants previously exposed to combined stress (mechanical + insect) led to a significantly 16.9-fold higher germination rate of *S. media* compared to the aqueous shoot extracts from untreated control plants.

Sinapis Alba *Shoot Extracts*

Relative to the aqueous control, the germination rate of both weed species showed a significant decrease of 37 to 81% through the application of all investigated aqueous *S. alba* shoot extracts. Compared to the shoot extracts produced from the untreated control plants, the application of shoot extracts obtained from phytohormonal, insect, and combined (mechanical + insect) treated *S. alba* plants resulted in significantly reduced germination rates in *A. myosuroides* and *S. media* of 64–65%, 35–38%, and 46–62%, respectively.

Chemical Analysis of the Aqueous Shoot Extracts

Total Phenolic Content (TPC) of the Aqueous Shoot Extracts

Both factors "Treatment" and "Plant species" and their interaction were significantly different regarding TPC ($p <$ 0.001). Among the plant species, the aqueous shoot extracts from untreated *A. strigosa* shoot biomass exhibited 2.6-fold significantly higher TPC compared to the shoot extract made from untreated *S. alba* (Fig. 6). Within the plant species, a 1.7-fold significantly higher TPC was measured in the aqueous shoot extracts of *C. sativa* under induced combined stress (mechanical + insect) compared to the shoot extracts from untreated *C. sativa*. In *S. alba*, insect-induced stress resulted in a significantly 1.9-fold higher TPC in the aqueous shoot extracts compared to those from untreated *S. alba*.

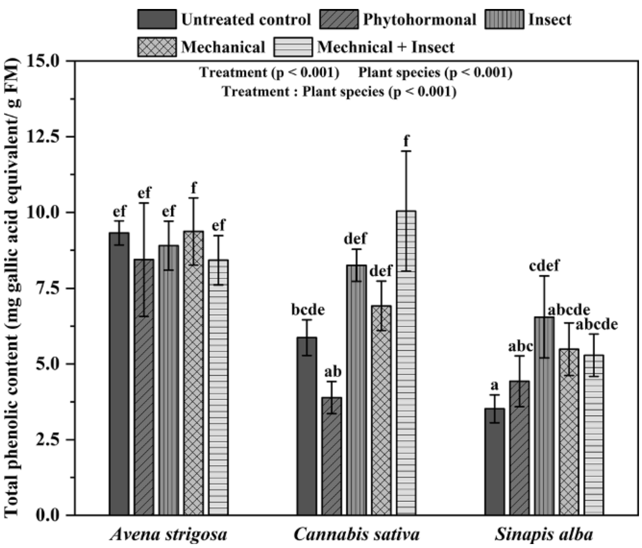

Fig. 6 Total phenolic content (mg gallic acid equivalent/g fresh matter) with standard deviations (SD) of aqueous shoot extracts from *Avena strigosa*, *Cannabis sativa*, and *Sinapis alba* shoot biomass treated under different stress conditions (+ untreated controls) at a concentration of 500 mg ml^{-1}. Mean values sharing the same letters are not significantly different based on the post-hoc test ($p < 0.05$). The *p*-values for the first factor 'Treatment', the second factor 'Plant species', and their interaction are shown. Treatments: Untreated control = untreated plants; phytohormonal = methyl jasmonate application; insect = *Hermetia illucens* paste application + mechanical leaf injury of the two oldest true leaves; mechanical = harrowing; mechanical + insect = harrowing + *Hermetia illucens* application

Chemical Analysis of the Aqueous Shoot Extracts by GC-MS/MS

Table 1 illustrates the percentage increase and decrease in peak areas of detected single phenolic compounds in aqueous shoot extracts derived from the shoot biomass of stress-treated *A. strigosa, C. sativa*, and *S. alba* plants using GC-MS/MS compared to the mean area peaks obtained from the untreated control plants.

Significant differences due to stress induction compared to the untreated control plants were measured in the aqueous *A. strigosa* shoot extracts only for the phenolic compound pyrogallol, where the phytohormonal induced stress resulted in significantly higher area peaks in the aqueous shoot extracts (Table 1).

In contrast, significant differences due to stress induction compared to the untreated control plants in the aqueous *C. sativa* shoot extracts were only measured for the phenolic compound salicylic acid, where no salicylic acid could be detected in the phytohormonally and combined (mechanical + insect) stressed *C. sativa* plants (Table 1).

In *S. alba*, however, significant differences were only detected for the phenolic compound *p*-hydroxy-benzyl alcohol, which was significantly higher in the aqueous *S. alba* shoot extracts prepared from the phytohormonally stressed plants than in the aqueous shoot extracts from the untreated plants (Table 1).

Discussion

Impact of Stress Treatments On the Physiological Processes of Avena Strigosa, Cannabis Sativa *and* Sinapis Alba

Our study showed that the effect of the investigated applied stresses on plant physiological processes varied between the three plant species. On the one hand, the maximum quantum yield of PS II of the investigated plant species was minimally affected by the stress treatments, in the case of *A. strigosa* and *C. sativa* or not affected like in *S. alba*. On the other hand, the induced stresses only had significant negative effect on the shoot biomass production of *C. sativa*. It was also shown that a combination of stress types tends to lead to a greater reduction in shoot dry matter than the single applied stress types. One reason for the minimal impact on the physiological processes in the investigated three plant species could be the low intensity of the applied stresses and the single stress application. Another reason could be the early measurements after the stress treatment, which may have missed stress responses that could occur in later stages of plant growth.

Several studies indicate that the effects of stress treatments on plant PSII and biomass production vary depending on factors such as plant species, type and dosage of the stressor, and the time of measurement after the stress treatment (Fatma et al. 2021; Sirhindi et al. 2020; Welling et al. 2023; Quan et al. 2023; Farooq et al. 2016; Kruidhof et al. 2014). However, to avoid potential long-term impairment of biomass production and PSII activity, the type and intensity of stress should be carefully selected to ensure that plant physiological processes are only minimally affected, as shown in this study. This is particularly important to achieve high quantities of shoot biomass and ensure good plant development, which are both essential for effective weed control in cover cropping.

In addition, the three types of stress investigated differ in their mode of action but had minimal or no effect on the physiological processes of the three plant species in this study for the reasons mentioned above.

MeJA is known to activate enzymatic antioxidants, which protect the photosynthetic apparatus (Fatma et al. 2021), enhance chlorophyll content and CO_2 assimilation (Sirhindi et al. 2020), but, additionally, can suppress mitosis, leading to reduced plant growth and biomass production (Sun et al. 2013; Patil et al. 2014).

Harrowing causes injury to plant organs, inhibiting growth and biomass production, and affecting PSII by

Table 1 Percentage (%) increase (+) and decrease (–) in peak areas of detected phenolic compounds by GC-MS/MS within the aqueous shoot extracts of the shoot *biomass of the treated plants (phytohormonal (Ph) = MeJA application*; insect (In) = *Hermetia illucens* application; mechanical (Mech) = harrowing; mechanical + insect (Mech + In) = *Hermetia illucens* application + harrowing) *Avena strigosa,* Cannabis sativa, and *Sinapis alba* with standards deviations, compared to the mean within the aqueous shoot extracts of the untreated control plants (Control), five days after stress induction. If the phenolic compound could not be detected in the aqueous shoot extract by GC-MS/MS, the abbreviation n. d. was used. Mean values within a plant species and within a single phenolic compound sharing the same letters are not significantly different based on the post-hoc test ($p < 0.05$). The *p*-values for the factor 'Treatment' within a plant species and within a single phenolic compound are shown

		Phenolic compounds												
Plant species	Treat-ment	Butylated Hydroxy-toluene	p-Hydroxy-benzyl alcohol	3,4-Di-hydroxy-benzoic acid	Gallic acid	p-Hydroxy-phenylacetic acid	Ferulic acid	Salicylic acid	Vanillic acid	β-Hydroxy-butyric acid	Benzoic acid	Pyrogallol	Catechol	2-Methyl-benzoic acid
A. strigosa	Control	0.0 ±91.1	0.0 ±92.2	0.0 ±88.7	0.0 ±71.9ab	0.0 ±92.8	0.0 ±89.1	0.0 ±87.9	0.0 ±173.2	0.0 ±54.0	0.0 ±28.6	0.0 ±173.2b	0.0 ±147.9	0.0 ±173.2
	Mech	–14.6 ±88.8	–65.3 ±5.4	–61.7 ±32.1	+174.8 ±124.5a	–71.9 ±36.0	+41.8 ±123.0	–7.0 ±67.3	–29.7 ±121.8	–56.7 ±15.9	–28.9 ±62.0	+71.9 ±89.7ab	–1.1 ±135.8	–100 ±0.0
	Ph	–100 ±0.0	–57.0 ±22.0	–26.8 ±60.3	+125.8 ±30.5ab	–56.3 ±75.8	–100 ±0.0	–5.7 ±18.1	–100 ±0.0	+238.2 ±331.4	+6.8 ±22.1	+873.2 ±614.4a	–100 ±0.0	–52.4 ±82.5
	In	–46.0 ±93.5	–61.7 ±34.1	–96.9 ±0.9	–84.5 ±26.9b	–95.1 ±4.4	–100 ±0.0	–44.2 ±51.0	+144.0 ±212.0	–100 ±0.0	–83.1 ±29.2	–58.8 ±35.7b	–100 ±0.0	+28.3 ±111.1
	Mech +In	–33.3 ±115.5	–47.2 ±20.9	–22.9 ±37.5	+2.9 ±91.7ab	+136.0 ±408.7	+44.3 ±127.6	–9.4 ±27.2	+134.2 ±405.7	–79.6 ±17.8	–44.4 ±55.4	+76.2 ±207.8ab	–92.4 ±13.2	+0.5 ±174.0
	p-value	*0.684*	*0.447*	*0.261*	*0.014*	*0.607*	*0.169*	*0.875*	*0.629*	*0.107*	*0.144*	*0.009*	*0.430*	*0.740*
C. sativa	Control	0.0 ±98.2ab	n. d.	n. d.	n. d.	n. d.	n. d.	0.0 ±52.9a	n. d.	n. d.	0.0 ±173.2	n. d.	n. d.	0.0 ±86.6
	Mech	+68.1 ±51.2a	n. d.	n. d.	n. d.	n. d.	n. d.	–78.7 ±36.8ab	n. d.	n. d.	–5.0 ±83.7	n. d.	n. d.	+75.7 ±25.9
	Ph	–100 ±0.0 b	n. d.	n. d.	n. d.	n. d.	n. d.	–100 ±0.0b	n. d.	n. d.	+17.0 ±202.6	n. d.	n. d.	+12.1 ±100.1
	In	–45.5 ±94.5ab	n. d.	n. d.	n. d.	n. d.	n. d.	–68.9 ±53.9ab	n. d.	n. d.	–100 ±0.0	n. d.	n. d.	+73.1 ±4.6
	Mech +In	–100 ±0.0b	n. d.	n. d.	n. d.	n. d.	n. d.	–100 ±0.0b	n. d.	n. d.	–8.3 ±158.9	n. d.	n. d.	–61.2 ±67.2
	p-value	*0.035*	–	–	–	–	–	*0.046*	–	–	*0.865*	–	–	*0.150*
S. alba	Control	0.0 ±53.2	0.0 ±47.4b	n. d.	n. d.	n. d.	n. d.	0.0 ±94.1	n. d.	n. d.	0.0 ±173.2	n. d.	n. d.	0.0 ±9.3
	Mech	–19.5 ±78.0	–70.1 ±7.8b	n. d.	n. d.	n. d.	n. d.	–67.7 ±56.0	n. d.	n. d.	–100 ±0.0	n. d.	n. d.	–35.1 ±56.6
	Ph	–6.3 ±81.3	+198.2 ±37.3a	n. d.	n. d.	n. d.	n. d.	–80.4 ±34.0	n. d.	n. d.	+53.2 ±256.3	n. d.	n. d.	+19.8 ±24.1
	In	–41.1 ±52.7	–0.6 ±122.8b	n. d.	n. d.	n. d.	n. d.	+91.9 ±207.1	n. d.	n. d.	+31.5 ±227.8	n. d.	n. d.	+18.3 ±9.4
	Mech +In	–66.8 ±57.5	–41.0 ±19.5b	n. d.	n. d.	n. d.	n. d.	–42.9 ±49.6	n. d.	n. d.	+28.7 ±222.9	n. d.	n. d.	–0.8 ±2.8
	p-value	*0.723*	*0.003*	–	–	–	–	*0.354*	–	–	*0.890*	–	–	*0.195*

damaging chloroplasts, increasing reactive oxygen species, and reducing photosynthetic electron transfer and the maximum quantum yield of PSII (Quan et al. 2023).

In contrast, the application of insect stress (including the combined stress) was the only stress treatment in this study that resulted in localized necrosis, which were limited to the respective application areas in all plant species without spreading. The observed hypersensitive response, characterized by local cell death due to dehydration, showed symptoms similar to those caused by burndown contact herbicides such as formulations containing fatty acids like pelargonic acid (Ciriminna et al. 2019). Therefore, we assume that the observed symptoms may be attributed to the presence of lipids, particularly unsaturated and saturated fatty acids, which constitute up to 17% of the total weight of the investigated adult *H. illucens* (Leyva-Gutiérrez et al. 2022). Phytotoxicity has been reported for saturated fatty acids, such as lauric acid, palmitic acid, and stearic acid (Fukuda et al. 2004; Cruz-Estrada et al. 2019), which are major components of saturated fatty acids within adult *H. illucens* biomass (Leyva-Gutiérrez et al. 2022). Furthermore, other authors have observed reduced PSII activity due to insect infestation associated with physical injuries caused by sucking, biting, and chewing insects, resulting in increased water loss from the injured plant tissue (Aldea et al. 2005), reduced leaf water potential due to damaged vascular bundles (Nabity et al. 2009), and closure of the stomata (De Freitas Bueno et al. 2009). Therefore, the observed reduction in *C. sativa* shoot dry matter due to insect stress can be explained by the mechanical damage to the leaves and the phytotoxic fatty acids in the applied *H. illucens* paste.

Nevertheless, the well-functioning stress response observed in all plant species in our study suggests that any reduction in their competitive ability against weeds, due to impairment of photosynthesis and biomass production, may be minimal or nonexistent a few days after the application of the three investigated stress types.

Impact of Stress Treatments On the Allelopathic Potential and Total Phenolic Content of Avena Strigosa, Cannabis Sativa *and* Sinapis Alba *Shoot Tissues*

All aqueous shoot extracts prepared from the untreated and treated plants inhibited germination and root growth of the three investigated plants, with few exceptions in *T. aestivum*. This suggests that the small seeded weed species were more influenced in the germination and root growth than the larger *T. aestivum* seeds. Aliotta et al. (2006) explained in their studies that small seeds, such as the investigated weed seeds, have a larger surface-to-volume ratio, thus being more intensively exposed to the extracts and consequently exhibiting a stronger influence on germination rate and root growth. The bioassay revealed that all aqueous shoot extracts inhibited weed root length of the two weed species more strongly than the germination rate. This aligns with previous research, which has found that radicle growth tends to be more susceptible to aqueous shoot extracts than seed germination (Rueda-Ayala et al. 2015; Patanè et al. 2023).

Phytohormonal Stress Treatment Of all stress treatments, the application of MeJA increased the inhibiting effect of *C. sativa* and *S. alba* shoot extracts on the seed germination and root growth (only in *T. aestivum*) the greatest with a tendency to a reduced total phenolic content (TPC) in *C. sativa* or increased TPC in *S. alba*. Literature reports that MeJA effects on TPC within the plants vary, depending on plant species, plant age, dosage (concentration and application frequency) and time of sampling after the stress application. For example, Gabotti et al. (2019) measured an increase in TPC (+42%) in *C. sativa* tissue cultures four days after the MeJA application (0.1 mg ml^{-1}). Furthermore, Kim et al. (2006) observed an increase (+41%) in TPC in 7 days old shoots of *Raphanus sativus* L. 12 h after MeJA application (0.22 mg ml^{-1}) and primarily identified the phenolic compounds ferulic acid, isoferulic acid, sinapic acid, methyl ferulate and methylsinapate in the shoot extracts. Several studies indicate that MeJA application can mimic pathogen infestations, supporting systemic defence responses through systemic and local activation of late and early response genes (Howe 2004), and resulting in increased production of proteinase inhibitors and allelopathic plant secondary metabolites (Farmer and Ryan 1990; Kim et al. 2006; Doughty et al. 1995; Aerts et al. 1994). Conversely, the application of high concentrated MeJA formulations can lead to a reduced TPC, as shown in our study in *C. sativa*. Similar observations were made by Salitxay et al. (2016), who measured a reduced TPC in 16-day-old *Hordeum vulgare* L. seedlings after two time-shifted high concentrated MeJA applications (1 mg ml^{-1} on day 10 and on day 13). Additionally, the enhanced phytotoxicity of shoot extracts from MeJA-treated *C. sativa* and *S. alba*, along with the reduced (in *C. sativa*) or slightly increased (in *S. alba*) TPC, suggests a relocation of the plants to the production of non-phenolic phytotoxic secondary metabolites such as alkaloids, cannabinoids, and terpenoids in *C. sativa*, and glucosinolates and their hydrolysis products in *S. alba*. However, this could not be confirmed in the present study due to the lack of further specific chemical analyses for these secondary metabolites. In addition, these plant metabolites remained undetected by GC MS/MS analysis because the focus was solely on phenolic compounds. Nevertheless, other studies have shown that MeJA treatments can increase the phytocannabinoid content in the bracts and flowers of *C. sativa* (Bailey 2019, Garrido et al. 2022), the triterpenoid content of hairy root cultures in *C. sativa* (Kobtrakul et al. 2023), and the glucosinolate content in Brassicaceae shoots (Baenas et al. 2014). In contrast to *C. sativa* and *S. alba*, MeJA application in *A. strigosa* resulted in reduced phytotoxicity of the aqueous shoot extracts compared to the shoot extracts from the untreated plants, which can be explained on the one hand by the slightly reduced TPC and the strongly increased pyrogallol content in the shoot extracts from the MeJA-treated plants. Pyrogallol can stimulate seed germination, as shown by Hendricks and Taylorson (1975) in their study with *Lactuca sativa* L. and *Amaranthus albus* L.. The authors assume that pyrogallol promotes seed germination by inhibiting catalase, which increases the concentration of H_2O_2 and thus supports NADPH reoxidation in the pentose phosphate pathway (Hendricks and Taylorson 1974).

Mechanical Stress Treatment In *A. strigosa*, the most effective stress type in this study was harrowing, as it was the only stress treatment that significantly increased the germination-inhibiting effects of the shoot extracts on both weeds and the cereal *T. aestivum*. However, since the mechanical stress treatment in *A. strigosa* showed no effect on the TPC we assume that harrowing may have increased the content of non-phenolic phytotoxic secondary plant metabolites such as avenacosides (saponins), which are present in the shoot biomass of *Avena* spp. (Papadopoulou et al. 1999). Due to a lack of chemical tests on individual saponins, this assumption could not be confirmed in the study.

Insect and Combined Stress Treatment Insect and combined stress increased, in most treated plant species, the germination-suppressive effects of the aqueous shoot extracts when applied to weed seeds. Additionally, both stress types were associated with an increased TPC in the shoot extracts of *C. sativa* and *S. alba*, while the TPC in the *A. strigosa* shoot extracts remained unchanged. Plants with generally high allelopathic potential and active allelochemical release, such as *A. strigosa*, are less sensitive to abiotic and biotic stress because their allelochemical defence mechanisms suppress competing weeds, reducing resource competition and enhancing their overall competitive ability (Olofsdotter et al. 2002). This increased competitiveness results in healthier plants, which are better equipped to withstand environmental stressors (Olofsdotter et al. 2002). Nonetheless, insect stress and combined stress appear to be the most effective stress types in this study for increasing allelopathic potential against weeds in *C. sativa* and *S. alba* at an early developmental stage. Other authors, however observed a decreased (Lamparski et al. 2015; Eleftherianos et al. 2006; Khattab 2007) or an increased (Prabu et al. 2023; Kumar et al. 2017; Palial et al. 2018) TPC through insect infestations, depending on the investigated insect and plant species. It is known that herbivore and pathogen infestation damage plant tissues and stimulate phenylalanine ammonia-lyase activity, which is crucial for phenolic compound biosynthesis (Dixon and Paiva 1995; Croteau et al. 2000). Thereby, most phenolic compounds are products of the phenylpropanoid metabolism, derived from the aromatic amino acids phenylalanine and tyrosine, which are derivatives of the shikimic-chorismic acid pathway (Croteau et al. 2000). However, after insect infestations, among all secondary metabolites, the accumulation of phenolic substances in plants is most noticeable (Wang et al. 2019).

Adaptation of the Investigated Stress Treatments for Future Practical Field Applications

Since this study only examined the stress types in greenhouse experiments, several aspects need further research before the practical application of artificially-induced stress in the field may be feasible. Nonetheless, certain general aspects should be considered to facilitate successful future field implementation of this management strategy:

1. The induced insect stress using *H. illucens* paste from adults should be replaced by an extract derived from the biomass of the adults, containing the phytotoxic substances, for effective and practical field implementation.
2. In most plants, allelochemical contents initially increase during early growth stages without stress, reaching a peak that subsequently declines over time (Aulakh et al. 2001; Reberg-Horton et al. 2005). Similarly, stress induction initially elevates the allelochemical content within plants within hours or days, achieving a maximum before decreasing over time (Baldwin 1994; Kruidhof et al. 2014). Moreover, allelochemicals in soil are influenced by climatic conditions and various factors, including biological, chemical, and physical soil properties, affecting their synthesis, persistence, distribution, and ultimately their phytotoxicity (Scavo et al. 2019). Consequently, multiple stress inductions during the vegetative phase may be necessary to achieve consistently high allelochemical levels in the soil during the growing phase and ultimately increase the allelochemical content in the plant residues, which is an important aspect in cover cropping.
3. In practice, one primary goal in cover cropping is to achieve effective weed suppression in the subsequent main crop, emphasizing the significance of allelopathic activity per unit area (Kruidhof et al. 2014). This activity results from a combination of CC biomass per area and allelopathic activity per unit biomass (Kruidhof et al. 2014). Therefore, stress induction must still facili-

tate maximizing biomass production of CCs, especially when applied multiple times or at high intensity.

Conclusion

Our study highlights the potential of artificially induced stress to enhance allelopathic properties in three plant species, offering a promising management strategy for improving the weed control capabilities of CCs in sustainable agriculture. All three stress treatments had minimal or no impact on plant physiological processes, yet insect and combined stress significantly increased the TPC in *C. sativa* and *S. alba*, strengthening their allopathic potential against weeds. Additionally, all insect-treated plants exhibited visible symptoms on the treated leaves. Moreover, shoot extracts from plants exposed to phytohormonal stress, insect stress, and combined stress displayed stronger germination-inhibiting effects compared to extracts from untreated control plants, with weed seeds showing greater sensitivity than *T. aestivum*. These findings suggest that the strategic application of artificial stress could serve as a potential management strategy in cover cropping to enhance the allelopathic potential of CCs, particularly in the early growth stages, thereby reducing reliance on synthetic chemical herbicides and contributing to more sustainable weed management practices. Furthermore, the study highlights that further optimisation of the three stress types investigated, along with research into their practical field application, is necessary to provide more precise insights regarding their potential commercial use as a management strategy to enhance the allelopathic potential of CCs.

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