



Elucidation of allelopathic potentialities of an invasive plant *S. nodiflora* towards an aggressive weed mimosa and documentation of the contributing allelochemicals

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Abstract

Weeds are one of the major contaminants of a crop field and seriously hamper agricultural production. The synthetic weedicides used to control weeds affect both ecosystem functioning and human health. Thus, novel techniques, especially nature-based solutions, are in great need as a replacement for the chemical weedicides. The use of phytochemicals obtained from invasive species can be the best sustainable approach. They are known to be allelopathic plants, and their synthesised metabolites, i.e., allelochemicals, exhibit strong selective phytotoxic activity. Invasive taxa synthesise these unique metabolites as a method of niche specialisation or territorial signature that can be exploited biotechnologically for the development of alternative herbicides. The phytochemicals were extracted from leaves of *S. nodiflora* using different solvents and tested for their allelopathic potentiality on *Mimosa pudica* seeds. The different germination behaviour and seed biochemical parameters were noted. The allelochemicals were applied to seedlings, and the changes in standard physical and critical biochemical events were reported. The contributing allelochemicals were identified through bioassay-guided fractionation followed by GC–MS-based identification. In the present investigation, phyto-metabolites from methanolic extracts of leaves of *S. nodiflora* exhibit potent seed germination inhibition activity against mimosa and affect its normal external morphology and internal biochemical machinery. The T_{50} (time required for the germination of 50% seeds) value was prolonged, and the reduction in insoluble carbohydrates, nucleic acid, and protein contents, as well as amylase action, was observed. Stress-related antioxidant enzymes- catalase, and peroxidase were drastically reduced. The pigment profiles, i.e., chlorophyll a, b, and carotenoids, were critically lowered, whereas the degree of lipid peroxidation increased. Compared to the control, the common physical parameters related to shoot and root length, dry, and fresh weight were affected in treated seedlings. The major metabolites present in the methanolic extracts responsible for such a promising allelopathic activity were quinic acid, protocatechuic acid, gentisic acid, caffeic acid, and ferulic acid, etc. The allelochemicals of *S. nodiflora* can be employed for the development of alternative eco-friendly herbicides and also pave the way for the management of alien species.

Keywords Phytotoxic metabolites · *Synedrella nodiflora* · Soil science · Crop protection · Sustainable weed management

1 Introduction

Weeds are harmful pests, more than pathogenic fungi and bacteria, competing intensely with cash crops and depleting nutrients from fertile areas, resulting in a decline in the quality and quantity of agricultural products (Islam and

Kato-Noguchi 2013; Shixing et al. 2021; Aremu et al. 2024). Weed issues cost the Indian agricultural sector almost 11 billion USD. Particularly in some selected crops, such as *Arachis hypogea* (35.8%), *Glycine max* (31.4%), *Brassica nigra* (21.4%), *Oryza sativa* (21.4%), *Vigna radiata* (30.8%), *Sorghum bicolor* (25.1%), *Sesamum indicum* (23.7%), and *Pennisetum glaucum* (27.6%), weed contamination prevents the harvesting of a certain percentage of products (Gharde et al. 2018). Weeds outcompete crops and deplete nutrients from cultivable lands and other critical factors—light, water, and space—causing qualitative and quantitative deterioration of agricultural products. The contemporary options are none other than the use of chemical herbicides to control

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weeds in agricultural fields. These herbicides, when incorporated into the trophic and biomagnified, have strong side effects on both the environment and human health (Singh et al. 2009; Tarazona et al. 2017). They cause cellular-to-metabolic toxicity, neuroinflammation, and mitochondrial dysfunction, induce tumorigenesis and carcinogenesis, and block the reproductive pathway (Costas-Ferreira et al. 2022). Continuous application over time compromises the soil's biochemical parameters (pH, porosity, water holding capacity, organic content) and microbial load (population of beneficial plant growth-promoting rhizobacteria), thereby lowering agricultural productivity. Studies have reported that glyphosate, a widely used herbicide, can cause cholangiocarcinoma and non-Hodgkin lymphoma (Agostini et al. 2020). Therefore, there is a strong demand for substitutes for them with bio-based solutions (Pasaribu et al. 2017; Mushtaq and Fauconnier 2024). Here comes the role of phyto-metabolites from invasive alien species with natural allelopathic potential that can significantly contribute to the development of bio-herbicides (Senatore et al. 2007).

Allelopathy is the process by which plants produce and release specific chemicals, allelochemicals, into their surroundings through leaching, root secretion, and the decomposition of plant remains (Radivojević et al. 2025; Siyu et al. 2025; Al-Behadili 2025). They directly or indirectly impact adjacent plants' growth and metabolism, generally inhibiting them (Kostina-Bednarz et al. 2023). These are widespread among plants, and many wild and native types release allelochemicals as a way to establish their territory (Amiri et al. 2017; Islam et al. 2022). Allelochemicals have been extensively reported from invasive species (Suby et al. 2024). When introduced in an unknown habitat, alien species outcompete the native species through allelopathic interaction and use allelochemicals as weapons (Hussain et al. 2017; Li et al. 2021), which is why invasive species are considered the primary sources of allelochemicals (Macias et al. 2019). They primarily consist of phenolics, terpenoids, and alkaloids, and these unique compositions of metabolites can be employed along with synthetic herbicides in low dosages in intercropping, rotational cropping, green manures, etc., to cut down the usage of the chemical ones (Mennan et al. 2020; Aridi et al. 2025). Allelopathic effects of different invasive plants-*Bidens Pilosa*, *Ailanthus altissima*, *Coriandrum sativum*, *Chenopodium album*, and *Borreria latifolia* on a variety of test plants have been reported by several researchers (Li et al. 2025; Rajakumar et al. 2025; Bruno et al. 2025; Pannacci et al. 2025; Siyu et al. 2025; Al-sarai and Al-farttoosi 2025; Ferreira et al. 2025; Al-Andal et al. 2025; Cao et al. 2025; da Rosa et al. 2025 Zhang et al. 2025).

In the present investigation, herbicidal potentialities of allelochemicals of an invasive plant, *S. nodiflora* have been documented. The methanolic extracts were fractionated

through the bio-assay-guided method, and the major metabolites reported through the gas chromatography-mass spectrometry technique are caffeic acid, ferulic acid, luteolin-7-O-glucoside, rutin, parthenolide, artemisinic acid, costunolide, etc. These are known to interfere with cellular biochemistry. The content of protein-amino acid, soluble-insoluble carbohydrate gets altered. These metabolites block the enzymes responsible for antioxidative defense, i.e., amylase, catalase, and peroxidase. *S. nodiflora*, also known as Nodewood, is an herb of the Asteraceae and native to South and Central American countries, and it has been naturalized in some parts of Asia. Partial metabolome analysis reports the occurrence of various types of phenols, organic acids, flavonoids, alkaloids, etc. (Zheleva-Dimitrova et al. 2020). The leaf decoction is traditionally practiced for the treatment of rheumatism, and earache (Amoateng et al. 2021) and also used as a heavy metal (Cu, and Pb) detoxicant, bio-insecticide, and bio-fungicide (Susanto and Dwiati 2020). *S. nodiflora* has antimicrobial, antioxidative, anti-proliferative, anti-inflammatory, and immunomodulatory activity, etc. (Zheleva-Dimitrova 2020). Allelopathic potentialities have also been checked on different model plants- Radish (*Raphanus sativus*), and Mustard (*Brassica juncea*), tomato (*Lycopersicon esculentum* L. var. Vaishali), and brinjal (*Solanum melongena*, Wheat (*Triticum aestivum* L.) (Ghayal et al. 2013; Varpe 2019). The current study aims to evaluate the allelopathic potentialities of *Synedrella nodiflora* on an aggressive weed, *Mimosa pudica*, and identification of the allelochemicals, along with elucidation of the mode of action of the allelochemicals.

2 Material and methods

2.1 Collection of plant materials

Healthy and mature leaf samples of *Synedrella nodiflora* (L.) Gaertn. were obtained from Midnapore, Paschim Medinipur, West Bengal, India (22.4257° N, 87.3199° E). At first, the collected leaves were cleaned under running water to remove the adherent dust particles and dried. Seeds of *Mimosa pudica* L. were collected from the surroundings.

2.2 Extraction of allelochemicals

Initially, six different solvents- methanol, ethanol, chloroform, diethyl ether, n-hexane, and ethyl acetate were used to extract the allelochemicals, and the most potent one with the maximum allelopathic activity was selected for further studies. The methanolic extract exhibited the highest inhibition towards the test materials and was analysed further. In brief, 100 g of powdered leaves were mixed with 400 mL of methanol and shaken well for 48 h. The methanolic

solution was filtered, and the filtrate was concentrated in a rotary evaporator under low pressure. The obtained extract was lyophilized and run through a silica gel column (200 g, 100 cm × 3.5 cm), using hexane–ethyl acetate as a solvent. Ten different ratios of hexane and ethyl-acetate were applied, starting from absolute ethyl-acetate, and then decreasing the quantity of ethyl-acetate and increasing the quantity of hexane, i.e., Hexane: Ethyl-acetate (1:9, 2:8, 3:7, 4:6, 5:5, 6:4, 7:3, 8:2, 9:1, 10:0). 25 mL of each of these eluting solvents was run through the column. The eluted components, i.e., fractions, were collected in separate test tubes (40 test tubes, each having 12–13 mL of solutions) and tested for their individual seed germination inhibition properties (Pranjitha and Bai, 2024). The allelopathic potentiality of each of the collected fractions was evaluated by performing its seed germination inhibition test following the standard procedures, and the fraction that caused the lowest germination of seeds was carried for further studies (John et al. 2006). For the seed germination assay, 50 seeds of the test sample (*Mimosa pudica*) were taken for each group, and in total, three groups were made for each experiment. So, the data presented related to seed germination inhibition is obtained from 150 seeds. The assay was conducted in a Petri plate, and 25 seeds were placed in each plate.

2.3 Identification of allelochemicals

Out of different fractions of hexane–ethyl acetate, the most potent one, based on its allelopathic potentiality, was further analysed using Gas Chromatographic-Mass Spectrometry (GC–MS QP2010 Ultra, Agilent). The instrument was configured with a column flow of 1.21 mL/min. 2 µL of sample was injected in a split mode with an injection temperature of 260 °C. The ion source temperature was kept at 220 °C. m/z ratio scanning was performed from 40 to 650 for 35 min.

2.4 Impact of allelochemicals on the physical and biochemical parameters of the bioassay materials

The fraction with the maximum seed germination inhibition capacity was further tested on bioassay materials to detect the changes in their biochemical parameters. Levels of soluble and insoluble carbohydrates, protein, amino acid, nucleic acid, and activity of different enzymes catalase, amylase, and peroxidase on the control and treated seeds were measured following the standard protocols (McCready 1950; Moore and Stein 1948; Lowry et al. 1951; Snell and Snell 1971; Biswas and Choudhury 1978; Mitra and Basu 1979; Fick and Qualset 1975).

The Hexane–Ethyl Acetate (1:1) fraction was applied to the bioassay material, and changes in the physical and biochemical parameters of the seedlings were measured in

reference to the control. The treatment with allelochemicals starts when the plant reaches a maturity of 40 days. Next, the treatment (through foliar spray) is done in 2 phases: phase 1, a 30-day treatment, and phase 2, a 60-day treatment. Initially, both the phase 1 and phase 2 plants are distributed in four groups. Group I consists of the control plants, and Groups II–V are the treatment groups. The groups are as following- Group I-control set (without any allelochemical treatment), Group II-treated with allelochemicals (Hexane: Ethylacetate-9:1), Group III- treated with Hexane: Ethylacetate-8:2, Group IV- treated with Hexane: Ethylacetate-1:1, Group V- treated with Hexane: Ethylacetate-2:8. Both the two phases has these four types of treatment groups. After 30 days of treatment, the different physical and biochemical characteristics were estimated, and this was done for the 60-day treated plants. The experiment was repeated thrice, and in each case, three plants for each group were considered.

Lengths of stem, root, internodes, and pods were measured thrice from each set of plants, using a measuring scale. The number of leaflets, pods, flower, and nodules were also calculated. The stem circumference is measured with a measuring tape. Contents of proline, chlorophyll, carotenoids, malondialdehyde, and enzymatic activity of catalase, superoxide dismutase, and peroxidase were measured in the case of the treated and control seedlings (Lichtenthaler 1987; Lei et al. 2015; Abedi and Pakniyat 2010; Tyagi et al. 2017; Bibi et al. 2019). These data were collected from both 30-day and 60-day treated plants.

Initially, ten seeds were taken for each group, and upon their germination and emergence of seedling growth, the ones with the fastest emergence were taken for further experimentation. These plants were grown in large-sized black coloured grow bags (16 cm length and 25 cm height), and the loamy soil (sand: slit: clay-2:2:1) was used for their cultivation. No external fertilisers, and growth hormones were used, and watering was done as per the requirement (usually twice a day). The bags were placed in a shade house for proper radiation. No insecticides were sprayed. Foliar spray was done twice a day, in the early morning, post one hour of watering, and late evening-post one hour of watering with a quantity of 1 mL to 5 mL as per the growth phase. Usually, the allelochemicals are first dried (in a hot air oven at 30 °C overnight) to remove the solvent and then mixed with an equal amount of water (double distilled) and stirred thoroughly for the proper distribution, and then sprayed using a glass sprayer bottle.

2.5 Statistical analysis

All the experiments were performed in triplicate (n = 3), and the results are presented as means ± standard errors (SE). Data were analysed by Prism GraphPad software version

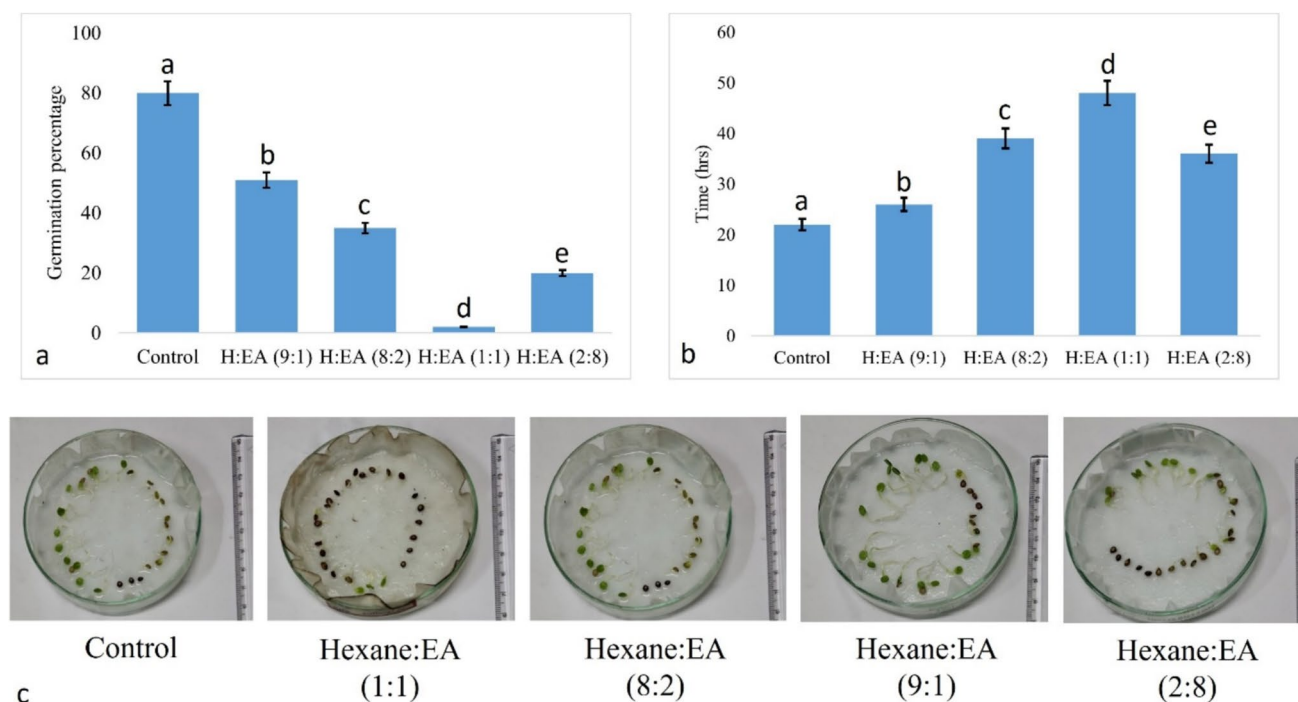


Fig. 1 Effect of different fractions of allelochemicals on the **a-** seed germination percentage, **b-** T_{50} value of Mimosa seed, and on the **c-** seed viability of Mimosa seedlings

9.2.0 (332) (San Diego, CA, United States). Tukey's multiple comparison test was performed at $P < 0.05$ to compare the mean differences. The different letters in the bar and column graphs indicate valid statistical differences between the treated and control sets.

3 Results and discussions

3.1 Allelochemicals inhibit the seed germination of the test plants

Allelochemicals obtained from the leaves of invasive plant *S. nodiflora* exhibit strong allelopathic activity. Different fractions of methanolic extract of allelochemicals were tested for their seed germination inhibition potential. Out of different fractions tested for their allelopathic activity; hexane: ethyl acetate (1:1) has the maximum degree of seed germination inhibition. It allowed only 5% seeds to germinate properly whereas in the control set, 81% of seeds germinated (Fig. 1a). The other fractions, i.e., hexane:ethyl-acetate- 9:1, 8:2, and 2:8 exhibited a seed germination percentage of 51, 37, and 23, respectively, which is remarkably lower than the control set (Fig. 1a). Such strong inhibition of seed germination indicates the strong allelopathic activity of the allelochemicals present in *S. nodiflora*. The time required for the germination of 50% of seeds is known as the T_{50} value. The

seeds present in the control set have a T_{50} of 22 h, whereas the treated sets have a T_{50} of 27, 39, 48, and 33 h, respectively, upon treatment with fractions having 9:1, 8:2, 1:1, and 2:8 ratios of hexane and ethyl-acetate (Fig. 1b). Here, the highest inhibition of seed germination in terms of T_{50} is observed in 1:1 treated seeds. The allelopathic potentiality of the allelochemicals of *S. nodiflora* is observed against the test plant seeds *Mimosa pudica* (Fig. 1c). A lower T_{50} indicates a healthy seed condition, whereas a lingered T_{50} reports the stress condition of the seed, and hampers of seed germination process. Thus, a lengthy T_{50} concludes that allelochemicals negatively interfere with the seed germination process and affect seed health.

The impact of allelochemicals on the physical conditions of the mimosa seedlings is recorded in Table 1. The root and shoot lengths of the control plants were 6.7 cm and 10.5 cm, 7.6 cm and 24 cm, respectively, after 30 and 60 days of allelochemical treatment. The root and shoot lengths were reduced in the treated seedlings (with hexane-ethylacetate-1:1) to 3.2 cm and 4.32 cm, 1.3 cm and 12 cm after 30 and 60 days of treatment. Other ratios, i.e., 9:1, 8:2, and 2:8, also had a negative impact on seedling growth, but the maximum reduction was observed in the case of the 1:1 treatment set. Leaflet numbers, stem circumference diameter, internodal length, number of nodules, and flowers were estimated, and these were found to be reduced in the allelochemical-treated sets and standard values in the

Table 1 Effect of *S. nodiflora* allelochemical on the common physical parameters of the Mimosa seedlings

	Control		9:1		8:2		1:1		2:8	
	30 days	60 days	30 days	60 days	30 days	60 days	30 days	60 days	30 days	60 days
Root length (cm)	6.7	10.5	5.98	7.23	4.3	6.54	3.2	4.32	4.1	5.32
Shoot length (cm)	7.6	24	7.12	22	6.29	20	1.3	12	5.82	18
Leaflet no	170	190	163	182	103	170	61	120	81	165
Stem circumference (cm)	0.3	0.6	0.3	0.54	0.15	0.52	0.11	0.28	0.23	0.43
Internodal length	2.2	6.4	2.01	6.39	1.62	5.80	0.4	3.32	1.20	5.51
Fresh weight (gm)	0.37	0.73	0.32	0.68	0.30	0.65	0.11	0.38	0.27	0.57
Dry weight (gm)	0.15	0.29	0.13	0.27	0.11	0.25	0.02	0.18	0.11	0.20
No of nodule	0	8	0	6	0	6	0	1	0	5
No of flower	0	7	0	5	0	3	0	2	0	3
No of pod	25	2			15		11			
Length of the pod (cm)	-	5.5		5.2		5.00	-	3.1		4.87
Breadth of the pod (cm)	-	0.12		0.11		0.11	-	0.09		0.11

non-allelochemical-treated sets. The number of pods, length, and breadth of pods were also reduced in the allelochemical-treated sets. In all the cases, the 1:1 hexane: ethyl acetate fraction is the most effective one and shows the highest allelopathic activity (Supplementary Fig. 1). The other ratios had a minute to moderate action. The growth of the treated plants was stunted. There was a noticeable reduction in dry weight. The leaves gradually become yellowish and face wilting. There were necrotic lesions that appeared on the leaf margin and spread along the midrib of the seedlings. The leaf tips drooped, and the premature senescence was due to the blockage of cell division.

The application of allelochemical triggers the degradation of pigments, i.e., chlorophyll a and b, followed by irregular stomatal opening (Cheema et al. 2004). Allelochemicals, once released into the soil, induce toxicity in the surrounding environment. This results in metabolic poisoning of the treated plants and causes a reduction in both root and shoot length (Li et al. 2010a, 2010b). Also, the plant-water relationship is hampered due to blockage in mineral nutrition, i.e., hampering of ion transport. This leads to the reduction of fresh biomass (Weir et al. 2004). The mechanism of allelochemicals to block the enzymatic (i.e., α -amylase, phosphorylase, etc.) interactions in a target plant is quite common and has been documented by several workers (Politycka and Gmerek, 2008). Generally, the phytotoxic components reduce the radicle length, causing a loss in dry weight, and block the nutrient absorption capacity of plants by restricting the vertical growth and cell division of roots (Xie et al. 2019). Also, the biochemical pathways (i.e., mitochondrial electron transport chain, and ATP production) related to respiration ceased, osmotic pressure changed, and common metabolisms of the chloroplast were affected (Einhellig et al. 2004). All of this stunts the seed germination and seedling growth. Shixing et al. (2021) reported the allelopathic

potentialities of an invasive weed *Solanum rostratum* Dunal, and documented twenty-nine volatile constituents (majorly-Phytol and cholesterol trimethylsilyl ether) with potent phytotoxicity towards the three common weeds, i.e., *Poa annua*, *Amaranthus retroflexus*, and *Medicago sativa*. Our investigational data also relates to the outcomes of Amiri et al. (2017) where the allelopathic potentiality of metabolites of *Pinus nigra* L. subsp. *Laricio* exhibits herbicidal potential against *Phalaris canariensis* L., *Trifolium campestre* Schreb. and *Sinapis arvensis* L. They choke the normal rates of seed germination, decrease vigor, and reduce radicle length and dry weight. They essentially restrict the vertical growth and cell division of the root system, which affects plants' nutrient absorption profile. The investigational results of Xie et al. (2019) in the case of *Echinochloa crusgalli* coincide with our data. Phytochemicals present in red and green leaves of *Rhus typhina*, *Ficus carica* L. cultivars, and sesame plants are reported to inhibit the seed germination and growth of lettuce (*Lactuca sativa* L.) and radish (*Raphanus sativus* L.) and two weeds peganum (*Peganum harmala* L.) and thistle (*Silybum marianum* L.), *Cyperus rotundus* L. (Wang et al. 2017; Ladhari et al. 2020).

3.2 Allelochemicals alter the pigment profile of test plants

The contents of chlorophyll a, and b, the major antenna pigment for photosynthesis, were found to be reduced after 30 and 60 days of treatment. In the control plants, the chlorophyll a content was 8.53 ± 0.78 , whereas in the treated sets, i.e., 9:1, 1:1, 8:2, and 2:8 (hexane ethyl-acetate fractions), the chlorophyll a content was reduced to 6.47 ± 0.82 and 11.32 ± 1.01 , 3.31 ± 0.11 and 6.12 ± 0.23 , 6.33 ± 0.71 and 8.93 ± 0.92 , 6.01 ± 0.60 and 7.99 ± 0.79 mg/g fresh weight after 30 and 60 days of treatment, respectively (Fig. 2a). The

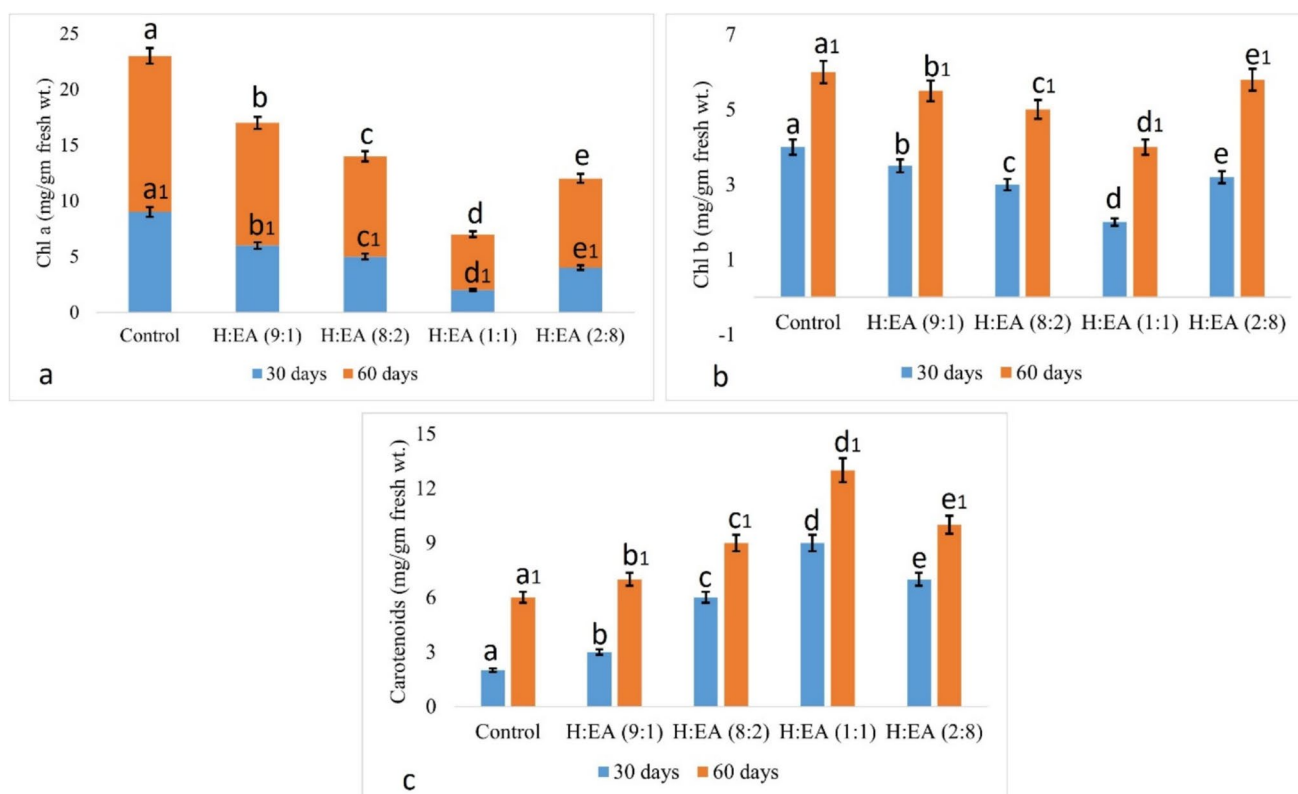


Fig. 2 Effect of different fractions of allelochemicals on the pigment profile i.e., **a**- Chl a, **b**- Chl b, and **c**- carotenoid content of the treated and control plants after 30 and 60 days of treatment

chlorophyll b content in the treated seedlings was reduced to 3.11 ± 0.62 and 5.53 ± 1.01 , 2.01 ± 0.31 and 4.09 ± 0.68 , 2.93 ± 0.61 and 5.34 ± 1.09 , 3.32 ± 0.77 and 6.23 ± 1.42 mg/g fresh weight upon treatment with 9:1, 1:1, 8:2, and 2:8 hexane ethyl-acetate fractions for 30 and 60 days, respectively (Fig. 2b). The major drop in chlorophyll a and b content was noted upon hexane: ethyl acetate (1:1) fraction treatment. There was a 2.57-fold and 1.85-fold reduction in these two pigment contents. Such a reduction indicates a drop-in photosynthetic activity of the allelochemical-treated plants.

The carotenoid contents in the treated seedlings increased, which is another proof of the breakdown of chlorophyll pigment components. In the non-allelochemical-treated seedlings, the carotenoid contents were found to be 2.78 ± 0.19 and 5.96 ± 0.67 mg/g fresh weight, whereas in the allelochemical-treated seedlings, the carotenoid content was increased to 3.13 ± 0.21 and 7.62 ± 0.52 , 8.78 ± 1.21 and 13.62 ± 2.23 , 5.76 ± 1.09 and 8.99 ± 1.21 , 6.29 ± 1.34 and 9.29 ± 2.98 mg/g fresh weight as a result of treatment with 9:1, 1:1, 8:2, and 2:8 fractions of allelochemicals after 30 and 60 days of treatment respectively (Fig. 2c). The major change was detected in the 1:1 fraction treatment, i.e., 3.15-fold and 2.28-fold enhancement was observed.

Chlorophyll a and chlorophyll b contents in the mimosa seedlings treated with H: EA (1:1) fraction were sharply reduced in both the 30-day and 60-day treated plants concerning the control set (Fig. 2a). A reduction in chlorophyll content may be due to either the inhibition of biosynthetic pathways of chlorophyll or the acceleration of the chlorophyll degradation process (Fig. 2a, b). Phytotoxic metabolites break the pyrrolic ring and phytol chain of the chlorophyll molecule (Gulzar and Siddiqui 2014). A drop of chlorophyll content blocks the normal processes of photosynthesis, and that is reflected in the production of photosynthate, e.g., glucose and various organic acids. The carbon skeleton of the cellular structures, the electron transport system, and the housekeeping genes involved in basic biochemical processes are blocked. To cope with the situation, the stored food materials are exhausted by the plant cells, and slowly, the normal cellular physiology is hampered. Carotenoids, in addition to chlorophyll, are also essential for autotrophs' process of uptaking and converting energy. This pigment serves as the main building block of the Light-harvesting Complex (LHC) and protects the photosynthetic apparatus (plant cells) against photooxidative damage, i.e., solarisation (Bryson et al. 2003). The carotenoid contents also show a significant shift in the treated sets in

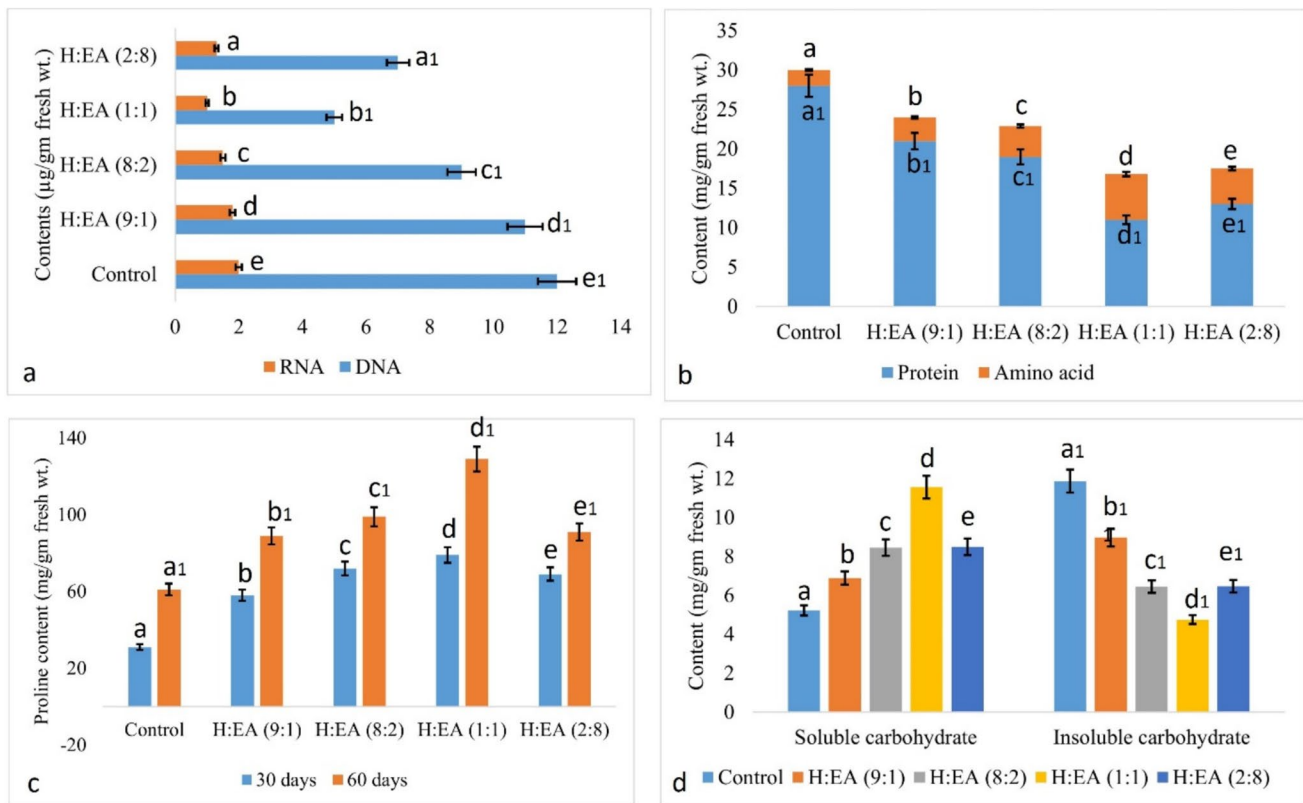


Fig. 3 Effect of different fractions of allelochemicals on the **a-** nucleic acid, and **b-** protein-amino acid content of the treated Mimosa seeds, and **c-** proline content of treated seedlings, and also **d-** soluble-insoluble carbohydrate content of the seeds

comparison to the control, which has a direct impact on the electron transport system (ETS) and causes severe photooxidative stress in the plant cells (Fig. 2c). 4-hydroxyphenyl pyruvate dioxygenase/phytoene desaturase is reported to be inhibited upon treatment with allelochemicals, which is a major intermediate in carotenoid biosynthesis (Romagani et al. 2000). Several reports include such chlorophyll degradation of weeds upon treatment with allelochemicals, e.g., allelochemicals of *Arbutus unedo*, *Medicago minima*, and *Myrtus communis* impact the growth and reproduction of *Aegilops geniculata* (Scognamiglio and Schneider 2020; Khamare et al. 2022).

3.3 Allelochemicals impact the essential biochemicals of Mimosa

The nucleic acid contents and protein-amino acid profile, concentrations of osmolytes (i.e., proline, soluble and insoluble carbohydrate) were found to be altered in the treated *Mimosa* seeds and seedlings. The amount of nucleic acid (DNA and RNA) in allelochemical-treated seeds is found to be reduced in comparison to the control seeds. In control seed the DNA and RNA contents are 12.13 ± 1.02 and 2.11 ± 0.09 µg/g fresh weight whereas upon treatment with

allelochemicals (different ratios of hexane:ethyl-acetate-1:1, 8:2, 2:8, 9:1) the values in the seeds dropped simultaneously, i.e., 5.15 ± 0.32 and 1.17 ± 0.04 , 9.39 ± 0.77 and 1.81 ± 0.05 , 6.49 ± 0.52 and 1.49 ± 0.05 , 11.14 ± 0.91 and 2.09 ± 0.07 µg/g fresh weight respectively (Fig. 3a). The hexane–ethyl-acetate fraction (1:1) had the maximum allelopathic activity and exhibited a 2.35-fold and 0.019-fold decrease in DNA and RNA contents.

In standard conditions (i.e., devoid of any stress), the free amino acid pool of a plant cell is at minimal quantities, whereas the protein contents remain high. Upon introduction of any stress, the situation gets reversed, the protein contents start to decrease, and the free amino acid content starts to rise. Here, the same situation has been witnessed. The application of allelochemicals leads to a reduction in amino acid contents and an increase in protein concentrations. In control seeds, the protein and amino acid contents were 26.69 ± 1.91 and 1.87 ± 0.07 mg/g fresh weight respectively, whereas in the treated sets, i.e., 1:1, 2:8, 8:2, and 9:1 fractions (hexane:ethylacetate) the values changed to 12.53 ± 1.07 and 6.23 ± 0.11 , 14.87 ± 1.21 and 4.79 ± 0.08 , 17.62 ± 1.39 and 3.92 ± 0.07 , 21.20 ± 1.67 and 2.99 ± 0.08 mg/g fresh weight respectively (Fig. 3b). Maximum effect

was seen when the 1:1 (hexane: ethylacetate) fraction was applied, i.e., a 2.13-fold decrease in protein content and a 3.33-fold increase in amino acid content were located in seeds, which signifies a severe allelopathic stress exerted by the allelochemicals.

There was an increase in proline content, which indicates the plant is facing stress, and to cope with that, the proline content is increasing. In the control seedlings, the proline content was found to be 27.79 ± 1.14 and 59.12 ± 2.08 mg/g fresh weight after 30 and 60 days of treatment, respectively. Upon treatment with allelochemicals, i.e., different ratios of hexane–ethyl acetate (1:1, 8:2, 2:8, 9:1), the proline contents increased but the maximum increase is detected upon treatment with the fraction of hexane: ethyl-acetate-1:1. So, this fraction has those allelochemicals that can cause the maximum harm to the treated plants. The proline contents in the control sets were 27.79 ± 1.14 and 59.12 ± 2.08 mg/g fresh weight, whereas the ones treated with 1:1 fraction had an elevated content of 79.91 ± 2.50 and 133.24 ± 3.31 mg/g fresh weight, i.e., 2.87-fold and 2.25-fold enhancement (Fig. 3c). The seedlings treated with the other fractions, i.e., 9:1, 8:2, and 2:8, have a content of 55.04 ± 1.80 and 88.53 ± 2.71 , 69.28 ± 1.17 and 99.13 ± 2.90 , 67.23 ± 2.13 and 88.29 ± 2.82 mg/g fresh weight after 30 and 60 days of treatment, respectively.

Another osmolyte insoluble carbohydrate, gets reduced in seeds after treatment with allelochemicals. Also, the contents of soluble carbohydrate get enhanced, and insoluble carbohydrate gets reduced. In the control sets, the soluble carbohydrate contents (5.19 ± 0.84 mg/g fresh weight) were reduced, and insoluble carbohydrate (11.72 ± 1.67 mg/g fresh weight) was high, which represents a healthy condition (Fig. 3 d). Upon treatment with different fractions of allelochemicals, the scenario changed, and the soluble carbohydrate content started to increase, and the insoluble carbohydrate content decreased, which represents the stress situation in the plant cell and cellular damage. The maximum reduction in insoluble carbohydrate pool (4.98 ± 0.72 mg/g fresh weight) and increase in soluble carbohydrate pool (11.01 ± 1.52 mg/g fresh weight) were observed when fraction-hexane: ethylacetate-1:1 was applied. So, there was a 2.12-fold enhancement in the soluble carbohydrate pool and a 2.35-fold reduction in the insoluble carbohydrate pool. The other fractions also had minute to aggressive effects, i.e., 2:8, 9:1, 8:2 hexane: ethyl-acetate ratios exhibited a soluble and insoluble carbohydrate contents of 8.37 ± 0.90 and 6.29 ± 0.80 , 7.24 ± 0.91 and 9.29 ± 1.19 , 8.39 ± 0.98 and 6.13 ± 0.92 mg/g fresh weight, respectively.

The change in nucleic acid and carbohydrate content evidences the strong interruption in biochemical events

(i.e., sugar metabolism and protein contents,) and central dogma process (i.e., premature termination of replication and translational pathways, troubling in karyokinesis and cytokinesis) caused by the allelochemicals present in the extract (Cheng and Cheng 2015; Mushtaq et al. 2019). Allelochemicals present in the lamiaceous weeds- *Hyp-tis suaveolens* (L.) Poit. and *Leucas cephalotes* (Roth) Spreng. exhibit similar types of phytotoxic mechanisms toward an aromatic rice, *Oryza sativa*-Gobindobhog (Oraon and Mandal 2021). Another example of cinnamic acid blocking the growth of cabbage seedlings by interfering with major biochemical steps also supports our present investigational outcomes (Singh et al. 2013). The profile of protein-free amino acids in the treated plants was found to be inversely proportional, which is indicative of the fact that proteins are getting degraded, and as a result, free amino acid contents kept increasing (Fig. 3b). Previous reports suggest that osmotic imbalance, acid–base inequality, and elevated reactive oxygen species (ROS) production are the primary causes of this (Thomason et al. 2018; Schandry and Becker 2020). Phytochemicals reported from maize plants exhibit allied types of stress towards soybean seedlings (Ahmad and Bano 2013). The proline contents of the treated plant were documented, and they indicated a noticeable surge in the treated seedlings after one month and two months of treatment (Fig. 3c). Not only in the seedling stage but also during the events of seed germination, there was a decrease in insoluble carbohydrates (Fig. 3d). These two components, i.e., proline and soluble carbohydrates, are the primary contributors to the osmoregulation of a cell that ameliorates the chemical stress in plant cells (Gulzar and Siddiqui 2014). Prolines serve several purposes, including initiating the Krebs cycle, preventing protein denaturation by maintaining water equilibrium, starting the manufacture of chlorophyll, and serving as an energy source (Hayat et al. 2012). An excess accumulation of both proline and soluble carbohydrates in the treated mimosa seeds is proof that the cells are trying to overcome the negative impact caused by *S. nodiflora* extracts. The impact of phytochemicals of tropical legume *Sesbania virgata* on the invasive plant- *Leucaena leucocephala* correlates with the present investigational outcome of seed carbohydrate metabolism (Mignoni et al. 2018). These phytochemicals interfere with seed germination, stop shoot and root growth, compromise quantum yield, i.e., decrease photosynthesis, lower the amount of chlorophyll, block the enzymatic activity, reduce mineral absorption, interact with translational pathways, cellular processes, etc. (Aslam et al. 2017). Our current reports are satisfied by the phytotoxic action of *Heliotropium foertherianum* foliar extracts on radishes (Abdulghader et al. 2008).

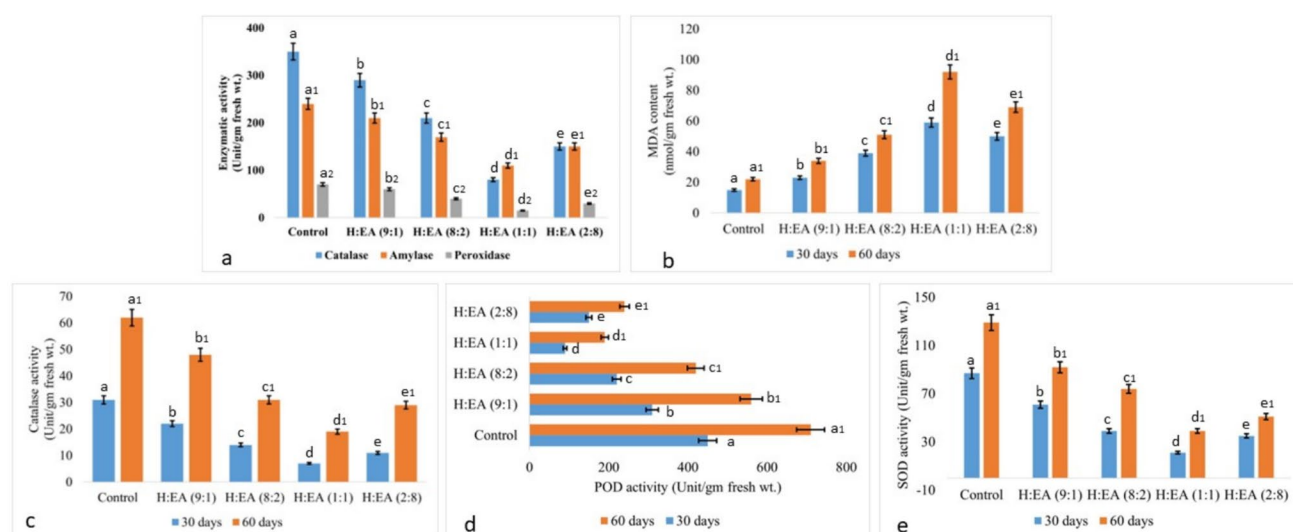


Fig. 4 Effect of allelochemicals on enzyme profiles of **a-** Mimosa seeds, and **b-** MDA content, **c-** SOD, **d-** POD, **e-** catalase activity of treated Mimosa seedlings

3.4 Allelochemicals of *S. nodiflora* block the enzymes involved in antioxidative defense

The allelochemicals obtained from *S. nodiflora* leaf extracts reduce the α -amylase, catalase, and peroxidase activity of the treated seeds in reference to the control. The seeds treated with allelochemicals (Hexani-Ethyl acetate-1:1) had a reduced catalase, α -amylase, and peroxidase activity of 91.17 ± 4.93 , 115.23 ± 5.01 , 9.91 ± 1.79 Unit/g fresh weight whereas the control seeds (without any treatment) had an enzyme activity of 337.19 ± 21.94 , 221.13 ± 16.10 , 61.70 ± 4.09 Unit/g fresh weight respectively (Fig. 4a). The other treated (Hexane-Ethylacetate-9:1, 8:2, and 2:8) seeds had reduced enzymatic activity in response to the control, but the maximum reduction is reported from Hexane-Ethylacetate-1:1 treatment. Application of hexane-ethyl-acetate (9:1) had a 293.24 ± 17.19 , 220.12 ± 9.93 , 55.72 ± 3.03 Unit/g fresh weight catalase, α -amylase, peroxidase activity, respectively. The other two treated sets, i.e., hexane-ethyl-acetate-8:2, and 2:8, had a reduced enzymatic (catalase, α -amylase, and peroxidase) activity of 225.49 ± 11.81 and 172.40 ± 8.27 , 181.20 ± 10.21 , and 173.91 ± 09.12 , 49.12 ± 2.09 , 19.21 ± 2.01 Unit/g fresh weight, respectively. In the most effective treatment set (i.e., hexane-ethylacetate-1:1), there was a 3.69-, 1.91-, and 6.22-fold decrease in the enzymatic activity.

The seedlings were treated with different ratios of allelochemicals, i.e., hexane: ethyl-acetate-9:1, 8:2, 1:1, and 2:8, and the treatments were continued for 60 days, and measurements were taken after 30 days and 60 days. The degree of lipid peroxidation occurring in the treated seedlings was estimated by measuring malondialdehyde content. The

hexane-ethyl acetate ratio of 1:1 was found to be the most effective in increasing the MDA contents. The MDA values were 18.10 ± 1.29 and 23.01 ± 1.70 nmol/g fresh weight in the control set after 30 days and 60 days of treatment. The values increased to 63.13 ± 4.58 and 91.23 ± 10.32 nmol/g fresh weight after 30 days and 60 days of treatment with hexane-ethyl-acetate (1:1) treatment, i.e., 3.49- and 3.96-fold enhancement in lipid peroxidation. The values were increased upon treatment with 8:2, 2:8, 9:1 hexane-ethyl-acetate up to 37.91 ± 2.30 and 51.09 ± 3.97 , 63.13 ± 4.58 and 91.23 ± 10.32 , 52.90 ± 4.01 and 61.08 ± 4.37 nmol/g fresh weight after 30 days and 60 days of treatment (Fig. 4b).

The change in catalase activity of the treated seedlings was measured. The control seedlings had a catalase activity of 31.11 ± 6.39 and 61.23 ± 9.81 Unit/g fresh weight after 30 days and 60 days of treatment. Whereas a treatment of hexane: ethyl-acetate (1:1) causes a catalase activity of 7.92 ± 1.03 and 18.32 ± 2.83 Unit/g fresh weight, leading to a 3.92-fold and 3.34-fold decrease. The seedlings treated with 2:8, 8:2, and 1:1 (hexane:ethyl acetate) allelochemical had a catalase activity of 11.29 ± 1.59 and 31.60 ± 5.19 , 14.20 ± 2.80 and 33.29 ± 6.83 , 7.92 ± 1.03 and 18.32 ± 2.83 unit/g fresh weight after 30 days and 60 days of treatment (Fig. 4c).

The peroxidase activity of the treated seedlings was detected after treatment. The control seeds had a peroxidase activity of 443.39 ± 39.20 and 779.13 ± 51.69 unit/g fresh weight after 30 and 60 days of treatment. The major effect is observed upon hexane: ethylacetate (1:1) treatment with an activity of 79.41 ± 5.30 and 193.91 ± 11.81 unit/g fresh weight, which indicates 5.58-fold and 4.01-fold reduction in enzymatic activity. The

hexane-ethylacetate (8:2, 2:8, and 9:1) treatment causes a reduction of up to 39.12 ± 5.91 and 73.20 ± 9.19 , 42.19 ± 6.02 and 59.90 ± 8.03 , 73.19 ± 10.32 and 127.39 ± 13.41 , respectively, after 30 days and 60 days of treatment (Fig. 4d).

The superoxide dismutase activity of the treated seedlings was detected in both treated and control seedlings. The activity was 73.19 ± 10.32 and 127.39 ± 13.41 unit/g fresh weight in the control set after 30 days and 60 days of treatment. The 1:1 ratio of hexane ethyl-acetate fraction exhibited maximum allelopathic activity in comparison to the other ratios tested. The activity was 3.48-fold (21.03 ± 2.09 unit/g fresh weight) and 3.42-fold (37.17 ± 4.10 unit/g fresh weight) reduced after treatment. The 8:2, 9:1, and 2:8 ratios yielded an activity of 39.12 ± 5.91 and 73.20 ± 9.19 , 57.09 ± 7.20 and 87.10 ± 10.43 , 42.19 ± 6.02 and 59.90 ± 8.03 unit/g fresh weight upon 30 days and 60 days of treatment (Fig. 4e).

An elevation in MDA levels signifies an augmented occurrence of peroxidation in the plasma membrane caused by the excessive buildup of ROS and a decline in the effectiveness of ROS-scavenging enzymes, such as SOD, POD, and CAT. The inability of SOD activity to detoxify ROS occurs simultaneously with the increase in MDA level. The formation of ROS in cells is a frequent biochemical occurrence and often does not cause significant harm, as they are promptly eliminated by the cellular antioxidant system. Exposing the plant cell to allelochemicals causes an excessive amount of stress, leading to an imbalance between the production and elimination of ROS (Radhakrishnan et al. 2018). The impact of fenugreek extracts on lettuce seedlings corroborates our current findings (Park et al. 2010). The presence of secondary metabolites leads to significant membrane damage, resulting in a substantial increase in MDA content. This increase in MDA content is directly associated with lipid peroxidation in the roots of cucumber and sorghum plants (Zeng et al. 2001). Allelochemicals induce an increase in the buildup of ROS in plants, resulting in harmful consequences. In the majority of situations, the plant's attempt to mitigate the damage employing antioxidant enzymes proves unsuccessful. The application of cinnamic acid, a powerful allelochemical, at a concentration of 400 mg L^{-1} , leads to a total inhibition of SOD activity in *Chrysanthemum coronarium*, consistent with the findings of our current work (Ma et al. 2020). A significant decrease in peroxidase activity impairs the overall health of the seedlings and disrupts a series of biochemical processes. POD serves multiple functions, such as regulating the levels of indole acetic acid and membrane permeability, stimulating cell wall formation and disease resistance, controlling oxygen supply to cells through the seed coat, and preserving seed dormancy.

3.5 Characterisation of the allelochemicals of *S. nodiflora*

Methanolic leaf extract was partially purified through silica gel column chromatography using different solvent ratios. Hexane and ethyl acetate at an equal ratio exhibited maximum seed germination inhibition compared to the other ratios tested. This fraction was subjected to identification through GC–MS (Fig. 5), and the components reported are presented in tabulated form (Table 2). The allelochemicals were detected within 8.905–28.277 min of run in the column. In total, ten allelochemicals were reported, i.e., quinic acid, protocatechuic acid, gentisic acid, caffeic acid, ferulic acid, Luteolin-7-O-glucoside, rutin, parthenolide, artemisinic acid, costunolide with a retention time of 8.9, 9.8, 10.6, 12.6, 21.1, 21.5, 22.6, 23.3, 23.6, 28.2 respectively. Rutin and protocatechuic acid were the phytochemicals detected in the sample with the highest and lowest molecular weights of 609.15 and $153.01 \text{ g mol}^{-1}$, respectively. There were initially 17 metabolites detected, but the ones with a higher probability (> 60%) have only been documented in the present study. Protocatechuic acid had the area percentage of 45.12% followed by artemisinic acid and costunolide with an area of 5.02 and 7.53%, respectively. So, these three metabolites are the major components of allelochemicals. Protocatechuic acid is a well-known allelochemical with strong phytotoxic activity against algal bloom-forming species *Scrippsiella trochoidea* (Chen et al. 2020). Another allelochemical, quinic acid, has also been reported earlier from *Cerbera manghas*, *Arbutus unedo*, *Medicago minima*, *Rhododendron capitatum*, and *Myrtus communis* with inhibitory activity against Dinophyta species, *Nitzschia Closterium*, *Aegilops geniculata*, *Elymus nutans*, *Poa pratensis*, *Medicago ruthenica*, and *Monostroma nitidum* respectively (Scognamiglio and Schneider 2020, Chen et al. 2021; Huang et al. 2023; Yang et al. 2024). Protocatechuic acid has been reported from different plants (*Sorghum bicolor*, and *Abutilon theophrasti*), also as allelopathic agents against a variety of plants, i.e., *Triticum aestivum*, *Zea mays*, *Phleum pratense*, *Lolium multiflorum*, *Echinochloa colona*, *Lepidium sativum*, *Medicago sativa*, and *Lactuca sativa* (Krumsri et al. 2020; Kakar et al. 2023; Shi et al. 2023). Rutin, present in the *S. nodiflora* extract, as detected from the present investigation, has been earlier detected from *Amaranthus spinosus* with strong inhibitory activity against *Oryza sativa* (Pengcheng et al. 2016). Caffeic acid, ferulic acid, and gentisic acid have been reported as potent allelochemicals from different allelopathic plants and exhibit phytotoxicity against some selected plants (Chen et al. 2022; Hussain and Reigosa 2021; Anwar et al. 2023; Li et al. 2010a, 2010b). Luteolin-7-O-glucoside, rutin, parthenolide, artemisinic acid, costunolide have been reported as potent allelochemicals by

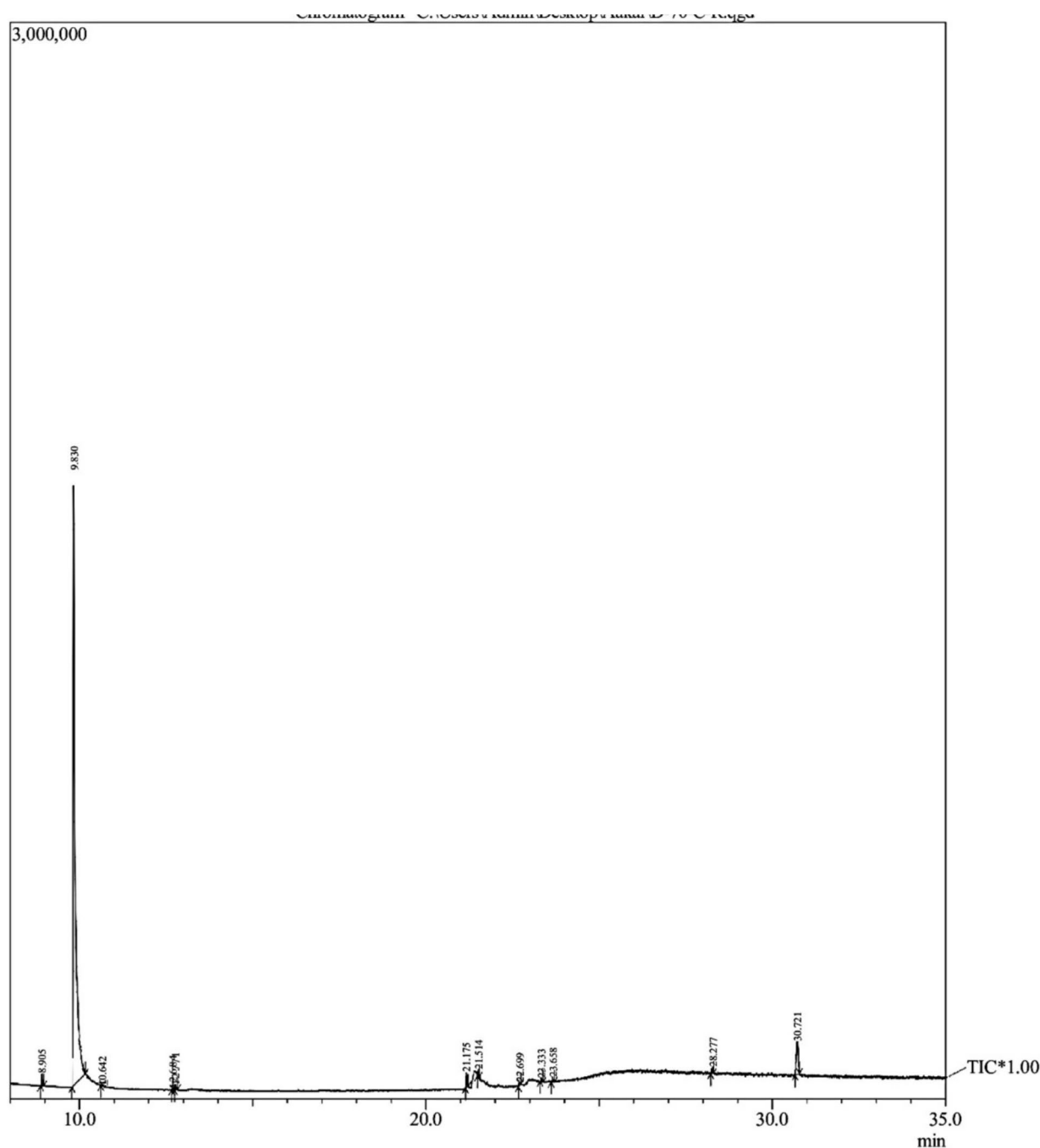


Fig. 5 GC–MS chromatogram of the allelochemicals present in the *S. nodiflora* hexane–ethyl acetate fraction (1:1) partially purified from methanolic leaf extracts

several researchers (Lydon et al. 1997; Macias et al. 1992; Abdelgaleil et al. 2009; Kostina-Bednarz et al. 2023).

These allelochemicals have not been identified earlier from *S. nodiflora*, but other phytochemicals have been reported with moderate to strong phytotoxic activities. Ghayal et al. (2013) reported ketone 3-(5-(1-(3-methylpentyl)oxy) propyl)-tetrahydro-2-oxofuran-3-yl)-dihydrofuran-2(3H)-one as the

prime phytotoxic chemical reported from *S. nodiflora* leaf leachate (Ghayal et al. 2013). Zheleva-Dimitrova et al. (2020) reported a different type of compounds from the same plant, including free fatty acids, triterpenoid saponins, phenyl ethanol glycosides, flavonoids, mono-di and triacylquinic acids, carboxylic acids, hydroxybenzoic acids, hydroxycinnamic acids, etc.

Table 2 Identification of potent allelochemicals of *S. nodiflora*

Sl. No	Name of the metabolite	Chemical formula	Molecular weight (g mol ⁻¹)	Retention Time (min)	Area (%)	Probability
1	Quinic acid	C ₇ H ₁₂ O ₆	191.0553	8.905	3.01	89
2	Protocatechuic acid	C ₇ H ₆ O ₄	153.0182	9.830	45.12	81
3	Gentisic acid	C ₇ H ₆ O ₄	153.0182	10.642	3.01	69
4	Caffeic acid	C ₉ H ₈ O ₄	179.0341	12.68	2.51	73
5	Ferulic acid	C ₁₀ H ₁₀ O ₄	193.0498	21.175	4.02	84
6	Luteolin-7-O-glucoside	C ₂₁ H ₂₀ O ₁₁	477.0931	21.514	5.02	96
7	Rutin	C ₂₇ H ₃₀ O ₁₆	609.1459	22.699	4.02	99
8	Parthenolide	C ₁₅ H ₂₀ O ₃	249.100	23.333	4.52	97
9	Artemisinic acid	C ₁₅ H ₂₂ O ₂	235.1694	23.658	5.02	68
10	Costunolide	C ₁₅ H ₂₀ O ₂	233.1537	28.277	7.53	80

4 Conclusion

In the present investigation, allelochemicals (i.e., quinic acid, protocatechuic acid, gentisic acid, caffeic acid, and ferulic acid) from methanolic leaf extracts of *S. nodiflora* exhibit strong allelopathic activity towards an aggressive weed, *Mimosa pudica*. The seed germination parameters of the *Mimosa* were affected through allelochemical treatment, i.e., the T₅₀ values prolonged, less seeds germinated in comparison to the non-treated ones, treated seedlings underwent excessive growth retardation in terms of physical and physiological aspects. The overall dry weight, leaf numbers, node-internode lengths, root and shoot lengths were compromised in the treated seedlings. The osmolyte balance (proline content), carbohydrate metabolism, pigment function, etc., of the mimosa seedlings were altered. The ratio of soluble and insoluble carbohydrates, DNA-RNA contents, and protein-amino acid contents was altered. The antioxidant defense-related enzymes, i.e., catalase, peroxidase, and superoxide dismutase, were elevated several-fold in both allelochemical-treated seeds and seedlings. The degree of lipid peroxidation (presented in terms of malondialdehyde contents) was reduced manifold in the treated seedlings than the non-treated ones. So, the allelochemicals inhibit the growth of *Mimosa* seeds/seedlings by exerting oxidative stress. Upon field validation through mixed cropping, the allelochemicals of *S. nodiflora* may function as bio-herbicides.

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Author contributions AP has performed the experiments, prepared the manuscript. PM supervised the whole work, made the critical planning and thoroughly checked the manuscript.

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Data availability The raw data and the biological materials are available and can be shared upon request.

Declarations

Ethics approval and consent to participate We have maintained the Institutional ethical guidelines while working with the plant species.

Consent for publication Both the corresponding author and the co-author have given their consent for publication.

Competing interests The authors declare that there is no competing interest related to the present study.

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