

Applied powdered leaf-biomass of alien weed *Hyptis suaveolens* (L.) Poit. in soil adversely impacts germination, growth, and yield of crop *Lens culinaris* Medik. despite enhancing soil fertility

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Abstract

Hyptis suaveolens L. (family Lamiaceae), an exotic fast-spreading invasive weed in Indian dry-tropics, was investigated for the allelopathic impact of its powdered leaf-biomass on the seed germination, growth, yield, photosynthetic-pigments and biochemical parameters (protein, proline and phenolic content) of the crop *Lens culinaris*. Soil characteristics (organic carbon, total nitrogen, available phosphorous and phenolic content) of soils amended with powdered leaf-biomass were also examined in this study. Soils were amended with differing doses (1g, 2g, 4g and 8g kg⁻¹ soil) of powdered leaf-biomass of the investigated weed. Lentil seed germination distinctly declined in soils amended with higher doses of powdered leaf-biomass. Crop growth, including its yield, significantly declined with increasing dose of powdered leaf-biomass. Compared to control, chlorophylls (a and b), carotenoids and protein content decreased significantly at varying growth stages of lentil with increasing dose. In contrast, proline and phenolic content in lentil crop significantly increased with increasing doses. The allelopathic index and synthesis effect of powdered leaf-biomass increased with increasing doses and it was significantly higher at the higher dose (8g kg⁻¹ soil). Thirty-five chemical compounds were GCMS-identified from the leaf extract of this weed. The identified compounds were mainly alkaloids, terpene, phenolics and fatty acids. Organic carbon, total nitrogen and phenolic content of the variously amended-soils increased significantly with increasing applied powdered leaf-biomass. In conclusion, powdered leaf-biomass of the *Hyptis suaveolens*, despite improving soil fertility, adversely impacted crop growth and its biochemical attributes, ostensibly through the release of allelochemicals, implying its immense invasibility in diverse ecosystems of India.

Introduction

It is well recognized the world over that the weeds cause a consequential threat to the indigenous plants and ecosystems through competition for growth resources with neighbouring native and crop plants (Lockwood et al. 2001; Hussain et al. 2019, 2020a). Invasive alien plant species (IAPS) show fast growth, high seed production, high allelopathic ability and high biomass production in very short duration, which facilitate them invading new areas (Kulmatiski 2006; Oliveira et al. 2016; Trognitz et al. 2016). Such invasive weeds adversely impact the agriculture production in terms of both quantity and quality (Gianessi and Reigner 2007; Rad et al. 2020). They may release various allelochemicals viz. flavonoids, phenolics, coumarin etc. which act as growth retardatory substances (Dayan and Duke 2014; Kumar et al. 2020; Karimmojeni et al. 2021). Alteration of soil characteristics on account of these substances and consequential microbial activities (Han et al. 2017; Latif et al. 2017), the altered edaphic environment often facilitates rapid colonisation of alien weeds which in the long run may eliminate the neighbouring plant species at ecosystem and species level (Chen et al. 2017; Kato-Noguchi 2020).

Several alien invasive plant species including *Hyptis suaveolens* (L.) Poit. with rapid colonisability and potential to adversely impact plant species growing in the vicinity (Padalia et al. 2014; Sharma et al. 2017) have been reported in Indian flora (Reddy 2008; Kumar et al. 2019). It is one of the fastest growing noxious aromatic annual weeds, rapidly invading diverse ecosystems in tropics and sub-tropics of the world (Afolayan 1993; Sarmiento 1984; Wulff and Medina 1971; Padalia et al. 2014). It is native to tropical America (Tang et al. 2019) and has been reported from different parts of India e.g. Vindhyan region, North-East India, Deccan Peninsula and Andaman and Nicobar Islands (Sharma et al. 2017) and Telangana region (Suthari et al. 2016). It generally grows luxuriantly in the months of July-November, along the railway tracks, roadsides and wastelands (Mudgal et al. 1997; Sharma et al. 2017). It is reported to have immense medicinal value, as it contains essential oils, alkaloids, flavonoids, phenols, saponins, terpenes and sterols (Ziegler et al. 2002). Its allelopathic potential can be attributed to chemical nature of the compounds released in soils that may concomitantly impact the survival of a plant species or the plant communities in vicinity. Although a considerable research has been carried out pertaining to the allelopathic influence of this weed on seed germination and seedling growth of several crops (Rodrigues et al. 2012; Poornima et al. 2015; Rao and Singh 2015; Arzoo et al. 2016; Sharma et al. 2019; Oraon and Mondal 2021), little is known about its impact on growth, yield and biochemical status of legume crops, particularly lentil (*Lens culinaris*) in Indian dry-topical conditions, which is one of the most important protein-rich legume crops, generally sown in winter season in India (Ram and Punia 2018; Saikenova et al. 2021). The investigation on impact of this aggressively advancing *Hyptis suaveolens* on lentil crop assumes immense importance in India and the world, as the total cultivated area of lentil in the world is estimated around 6.10 million ha with annual production and yield of 6.33 million tonnes and 1038 kg/ha, respectively (FAOSTAT 2019). India is the largest producer of lentil (Singh et al. 2022). It is cultivated in India on 5.2% of total area under pulses (29 million ha) contributing 6.7% of total pulse production (Malik et al. 2022).

There is relatively a dearth of ecological information on impact of *Hyptis suaveolens* on soil properties and lentil growth, as weed-biomass left over in fields may release various growth retardants that may adversely affect crop growth. It is hypothesized that decomposing weed-biomass may release various allelochemicals, which may directly or indirectly affect soil nutrient availability and plant growth. These allelochemicals are present in almost every part of a plant like root, leaf, stem, fruit, seed etc. and are released in soil during the process of their decomposition (Zimdahl 2018; Abate et al. 2021; Gupta et al. 2021; Mastinu et al. 2021). Of the different organs of the plant, leaves have been reported to contain more allelochemicals compared to that in other plant parts (Dorning and Cipollini 2006). Thus, the leaf

component of the *Hyptis suaveolens* weed used in the present study may be considered having immense allelopathic potential to influence the crop growth. These allelochemicals may also act as tools which help exotic invasive plants in their establishment and, in turn, invasion success in non-native habitats (Zheng et al. 2015; Uddin and Robinson 2017; Becerra et al. 2018; Ooka and Owens 2018).

The present study aimed to investigate the allelopathic impacts of varying doses of leaf-biomass of the invasive weed *Hyptis suaveolens* on: (1) the growth of lentil crop, (2) the biochemical status of lentil crop at its different growth stages, and (3) the physico-chemical characteristics of the amended soils.

Material and methods

Study species

Fresh leaves of *Hyptis suaveolens* (hereafter referred to as *Hyptis*) in its reproductive stage were collected in October 2018 from the weed-colonised study site, adjoining an agricultural field near Hasanpur (28°56'7.757" N latitude and 77°46'46.416" E longitude) in a dry-tropical region of Meerut in India. The leaves were washed several times with tap water, air-dried at room temperature for three weeks. Completely dried leaves were ground into fine powder, hereafter referred to as powdered leaf-biomass (PLB) and stored in autoclaved sealed polythene bags at room temperature for their use in pot experiments. The certified seeds of lentil (*Lens culinaris* Medik. variety Pusa Ageti) used in this study were obtained from Indian Agriculture Research Institute, New Delhi.

Pot experiments

The pot studies were conducted between December 2018 and March 2019 in the Department of Botany, Chaudhary Charan Singh University, Meerut (28°58'3.828" N latitude and 77°44'33.792" E longitude). The pots were kept under iron-netted cage (four sides open; roof-top covered by transparent polythene sheet). Maximum mean temperature (24.27°C) was recorded (12.00–2.00 pm) during the period of study. PLB of weed *Hyptis* was added at 1, 2, 4, 8 g/kg soil in pots separately in quadruplicates on 18 December 2018, each of size - top diameter 14.3 cm, bottom diameter 9.2 cm and 11 cm depth, filled with 1 kg of crop-field soil (pH 8.23 ± 0.02, conductivity 0.09 ± 0.003 mS, salinity 0.00 ppt, total nitrogen (%) 0.02 ± 0.001, organic carbon (%) 0.55 ± 0.005, available phosphorus (mg/g) 0.03 ± 0.002) for pot culture investigations. The PLB doses were decided on the basis of weed leaf-biomass estimated per unit area in weed-infested study sites. Unamended soil served as control. To study the allelopathic effects of different doses of PLB, a total of twenty pots (four for each dose) were prepared and labelled as H0 (control), H1, H2, H4 and H8. The digits suffixed to *Hyptis* code (H) indicated the amount (g) of applied PLB. An equal amount of tap water (100 ml) was added to each labelled pot to soak the soil and two days later *i.e.* on 20 December 2018, ten viable seeds of the recipient crop lentil were sown at the depth of 2–3 cm in each labelled pot. The experiments were carried out under shaded-house conditions with natural light supply, and pot positions were rotated to keep the environmental conditions uniform. An equal amount of tap water was added to each labelled pot from time to time, based on the soil requirements. Percent germination was recorded until no seeds germinated. Seed germination parameters, such as germination percentage (G%), mean germination time (MGT), mean germination rate (MGR), coefficient of variation of germination time (CV_t), germination index (GI), coefficient of velocity of germination (CVG) and germination rate index (AI-Mudaris 1998) were calculated according to Ranal et al. (2009). Twenty days after sowing (DAS), only three healthy individuals of the test crop lentil in each pot were allowed to grow for their growth estimates and the rest were eliminated. Periodically, the plant heights (cm) were measured with the help of a metallic tape at 20, 30, 40, 50, 60, 70 and 80 DAS. The test crop lentil was harvested at 90 DAS and oven-dried at 65°C for 48 hr. After harvesting, morphological parameters *viz* shoot-length, root-length, shoot-biomass (stem and leaf combined), root-biomass and yield-parameters, such as the number of pods/plant, number of seeds/plant, number of seeds/pod, pod-biomass (g), seed-biomass (g) and harvest index % (El Naim et al. 2010) were estimated.

Biochemical assays

Fresh leaves (randomly selected) were taken at different growth stages of the lentil plants: Initial (27 DAS), Intermediate (54 DAS) and Mature (81 DAS) in each labelled treatments (H0, H1, H2, H4 and H8) for studying the biochemical attributes and the sample extracts were recorded at different wavelengths (nm) using UV-1800 SHIMADZU Spectrophotometer. Chlorophyll a, b, total and carotenoid contents were determined according to Arnon (1949) and calculated as per Lichtenthaler (1987). Total protein (Bradford 1976), proline (Bates et al. 1973) and phenolic (Bray and Thorpe 1954) contents of lentil were analysed under the PLB-amended soils.

Allelopathic Index

The allelopathic response index (RI) of the weed-PLB was calculated according to Williamson and Richardson (1988). The synthesis effect (SE) of allelopathy were estimated using the mean of several RIs (germination%, shoot-length, root-length, shoot-biomass, root-biomass, number of pods/plant, number of seeds/plant, pod-biomass, seed-biomass and total biomass) value according to Zhang et al. (2019).

Soil analysis

After crop harvesting, soil samples were collected, air-dried and analysed for their physico-chemical characteristics that included pH, conductivity, total organic carbon (Walkley and Black method), total nitrogen (micro-Kjeldahl's method) according to Piper (1944), available phosphorus (Olsen et al. 1954) and total phenolic content according to Bray and Thorpe (1954).

Identification of allelochemicals

Methanolic extract was prepared from the *Hyptis* PLB following Netsere and Mendesil (2011). PLB of 7.50 g of the weed was extracted with 250 ml methanol in Soxhlet apparatus. The extraction continued till the solvent in the siphon tube of the extractor became colourless. Later, the extract was taken in a beaker and kept on a water bath at 62.5°C. This sample was maintained on a water bath till the final concentration was 1g/ml.

The chemical composition of the methanolic leaf extract was evaluated using a Thermo Scientific Trace 1300 Gas Chromatograph (GC) that was coupled with a Thermo TSQ 8000 Mass Spectrometer (MS) and a Thermo TG 5MS fused silica capillary column (30 m length × 0.25 µm diameter × 0.25 µm thickness). The starting oven temperature of 60°C was kept for 2 minutes before being raised to 250°C at a rate of 3°C / minute and held for 5 minutes. Helium, as the carrier gas, was employed at the flow rate of 1ml/minute. The volume of methanolic extract injected was 1 µl. Temperatures for the injector and transfer line were set at 250°C and 280°C respectively. The mass spectra were recorded using an injection split ratio of 1:150 and an ionisation energy of 70 eV throughout a scan mass range of m/z 50–600 amu. Compounds were identified comparing their mass spectra with those in the National Institute of Standards and Technology Mass Spectra Library and Wiley library.

Statistical analysis

Results were evaluated through one way ANOVA at 0.05, 0.01, 0.001 significance level and the difference among means was evaluated by the of Duncan test at 0.05 significance level using SPSS 20.0. The graphical analysis was carried out using MS Excel 2010.

Results

Impact on the seed germination attributes of crop

The amended soil with varying doses of PLB significantly ($p < 0.01$) affected the seed germination attributes of lentil crop (Table 1). The germination percentage decreased with the increasing doses of PLB. However, amongst the applied doses (H1, H2, H4 and H8) of PLB in the soil, it was noted that the doses of $\geq 2\text{g kg}^{-1}$ soil exhibited significant inhibition of lentil seed germination ($p < 0.05$). The germination index also showed a significant ($p < 0.05$) declining trend with increasing dose. Accordingly, mean germination time (MGT) increased with increasing PLB dose ($p < 0.05$). In contrast, other seed germination parameters *viz.* mean germination rate (MGR), germination rate index (GRI), coefficient of variation of germination time (CV_t), coefficient of velocity of germination (CVG) showed significant ($p < 0.05$) decreasing trend with increasing dose of applied PLB. The inhibition impact on lentil seeds was amply evident from the inhibition percentage recorded from 5 to 37% with increasing dose of weed PLB added to the soils.

Table 1

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on the germination parameter of lentil (*Lens culinaris*). Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). Mean values with same letter in the same columns indicate that they do not differ from each other by means of ANOVA compared to the Duncan test at 0.05 probability level.

Treatments	G (%) Mean ± S.E.	GRI (%/day) Mean ± S.E.	MGT (Days) Mean ± S.E.	MGR (%) Mean ± S.E.	GI Mean ± S.E.	CV _t (%) Mean ± S.E.	CVG Mean ± S.E.
H0 (Control)	100.00 ± 0.00 a	37.92 ± 6.14 a	3.10 ± 0.19 e	0.33 ± 0.02 a	159.00 ± 1.87 a	36.62 ± 3.30 a	32.60 ± 1.91 a
H1	95.00 ± 2.89 a	24.85 ± 2.13 b	4.40 ± 0.10 d	0.23 ± 0.01 b	138.75 ± 4.84 b	36.60 ± 0.52 a	22.77 ± 0.55 b
H2	87.50 ± 2.50 b	16.16 ± 0.28 c	6.08 ± 0.12 c	0.16 ± 0.003 c	113.00 ± 2.38 c	33.15 ± 1.37 a	16.48 ± 0.33 c
H4	80.00 ± 0.00 c	8.88 ± 0.38 d	9.56 ± 0.21 b	0.11 ± 0.003 d	75.50 ± 1.71 d	24.06 ± 1.80 b	10.47 ± 0.23 d
H8	62.50 ± 2.50 d	5.51 ± 0.35 d	12.16 ± 0.82 a	0.08 ± 0.01 d	42.25 ± 3.95 e	25.00 ± 2.76 b	8.34 ± 0.54 d
G(%): Germination percentage, GRI: Germination rate index, MGT: Mean germination time, MGR: Mean germination rate, GI: Germination index, CV _t : Coefficient of variation of germination time, CVG: Coefficient of velocity of germination							

Impact on the growth attributes of crop

The soil amended with different PLB doses showed a significant ($p < 0.001$) growth retardatory impact on the lentil plant length at different growth stages (Fig. 1). Shoot length inhibition significantly increased with increasing dose of PLB. However, this inhibition was less than the proportion in which the dose increased at any stage of the crop growth (DAS). Across different developmental stages, the highest inhibition of the crop growth was recorded at 30 DAS, across all respective applied doses ($p < 0.001$).

This decline in shoot lengths of lentil plants with increasing doses of PLB was also recorded for their length estimates at the end of the experiment (90 DAS) (Table 2). Shoot and root biomass of lentil plants also exhibited similar declining trend with increasing doses of PLB. The root length and root biomass of lentil decreased compared to the control, but a significant difference occurred only at the H8 dose of PLB. However, shoot biomass of lentil was significantly ($p < 0.05$) different from the control at H1 dose but the inter-dose difference for all applied PLB doses (H1, H2, H4 and H8) did not exhibit a significant level of change.

Table 2

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on the growth attributes of lentil (*Lens culinaris*) 90 days after sowing (DAS). Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). Mean values with same letter in the same columns indicate that they do not differ from each other by means of ANOVA compared to the Duncan test at 0.05 probability level.

Treatments	Shoot length (cm) (Mean ± S.E.)	Root length (cm) (Mean ± S.E.)	Shoot biomass (g) (Mean ± S.E.)	Root biomass (g) (Mean ± S.E.)
H0 (Control)	28.58 ± 1.41 a	19.57 ± 2.31 a	0.17 ± 0.01 a	0.04 ± 0.01 a
H1	26.35 ± 1.19 ab	14.81 ± 2.32 ab	0.12 ± 0.01 b	0.03 ± 0.01 a
H2	25.38 ± 0.85 ab	14.69 ± 1.24 ab	0.11 ± 0.02 b	0.03 ± 0.01 ab
H4	24.48 ± 1.30 bc	14.58 ± 1.61 ab	0.10 ± 0.02 b	0.02 ± 0.002 ab
H8	21.71 ± 1.22 c	12.55 ± 1.09 b	0.08 ± 0.01 b	0.02 ± 0.002 b

Yield of the test lentil plants also declined with increasing dose of applied PLB, albeit the significant decline ($p < 0.001$) was more conspicuous at the highest dose of 8g kg^{-1} in this study (Table 3). This declining trend of the crop yield was evident in the estimates of number and biomass of pods and seeds/plant. Harvest index also recorded a significant decline at the dose of 8g kg^{-1} soil ($p < 0.05$).

Table 3

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on the yield attributes of lentil (*Lens culinaris*) 90 days after sowing (DAS). Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). Mean values with same letter in the same columns indicate that they do not differ from each other by means of ANOVA compared to the Duncan test at 0.05 probability level.

Treatments	Number of pod/plant (Mean ± S.E.)	Number of seed/plant (Mean ± S.E.)	Number of seed/pod (Mean ± S.E.)	Pod Biomass (g) (Mean ± S.E.)	Seed Biomass (g) (Mean ± S.E.)	Harvest index (%) (Mean ± S.E.)
H0 (Control)	6.08 ± 0.68 a	11.92 ± 1.33 a	1.97 ± 0.03 ab	0.25 ± 0.01 a	0.24 ± 0.01 a	56.97 ± 2.45 a
H1	4.50 ± 0.63 b	8.58 ± 1.27 b	1.90 ± 0.04 ab	0.17 ± 0.02 b	0.16 ± 0.02 b	52.25 ± 4.51 a
H2	3.42 ± 0.56 bc	6.75 ± 1.10 bc	1.98 ± 0.02 a	0.12 ± 0.02 c	0.11 ± 0.02 c	45.89 ± 7.59 ab
H4	3.25 ± 0.51 bc	6.08 ± 1.00 bc	1.90 ± 0.08 ab	0.10 ± 0.02 c	0.08 ± 0.01 cd	42.83 ± 4.72 ab
H8	2.17 ± 0.35 c	3.67 ± 0.50 c	1.80 ± 0.08 b	0.06 ± 0.01 d	0.05 ± 0.01 d	37.20 ± 2.40 b

Impact on the photosynthetic pigments of crop

The soil amended with varying amount of PLB significantly ($p < 0.001$) affected the photosynthetic pigments (chl-a, chl-b, total chl and carotenoids) of the lentil crop plants at different growth stages (Fig. 2). Chlorophyll-a significantly ($p < 0.05$) decreased with increasing doses of applied PLB in all different growth (27 DAS, 54 DAS and 81 DAS) stage (Fig. 2a). The maximum reduction (56%) of chlorophyll-a was observed in intermediate growth stage (54 DAS) ($p < 0.05$) of lentil at H8 dose. However, no significant reduction was found between H4 and H8 doses in mature growth stage of lentil plants (81 DAS). Chlorophyll-b estimated at control (H0) was significantly higher than

those at H1, H2 H4 and H8 in initial and intermediate growth stages ($p < 0.05$). However, no significant difference was observed between control (H0) and H1 dose of PLB in mature growth stage (Fig. 2b). The maximum reduction of chlorophyll-b estimate (43%) was recorded in initial stage (27 DAS) at H8 dose. Total chlorophyll also significantly ($p < 0.05$) decreased with increasing doses of applied PLB at all the growth stages (Fig. 2c) and maximum reduction (51%) of total chlorophyll was found in intermediate growth stage (54 DAS) at H8 dose. The estimates of total carotenoids was also decreased significantly ($p < 0.05$) on the application of varying doses of PLB (Fig. 2d). In initial and mature growth stages of the lentil plants, total carotenoids decreased significantly ($p < 0.05$) at $\geq$ H1 doses. However this reduction was not significantly different at intermediate stage. The maximum reduction (68%) of carotenoid was recorded in initial (27 DAS) growth stage at H8 dose.

Impact on the biochemical status of crop

Investigation of the biochemical attributes in terms of total protein, proline and phenolic contents in the lentil crop under variously amended soils with the PLB exhibited varying trends (Fig. 3). Total protein content, in general, decreased compared to that in control (2–28%) with increasing dose (H1-H8) at all the three stages (27 DAS, 54 DAS and 81 DAS) of plant growth. However, this decrease was relatively more prominent and significant ($p < 0.001$) at the younger stage (27 DAS) of plant growth. In mature stage (81 DAS), the protein content recorded significant decrease ($p < 0.05$) at $\geq$ H4 doses (Fig. 3a).

In contrast to the increasing trend of leaf protein status of lentil plants with increasing doses of PLB, proline content (Fig. 3b) recorded a significant increase ($p < 0.05$) at every growth stage of the crop (initial, intermediate and mature). This increase varied from 18–436% (H1-H8 doses) compared to the control. This increase was relatively sharp and significant ($p < 0.05$) at higher doses ($> H2$).

Phenolic content, however, increased significantly ($p < 0.05$) with increasing PLB doses at all the three different growth stages (Fig. 3c). This increase varied from 12–89% (H1-H8 doses) compared to the control. At the matured stage of lentil crop growth, the phenolic content of the crop, showed significant inter-dose difference from H1 to H4. Despite increase in the phenolic content further at H8 at this mature growth stage, it lacked significant difference with H4.

Allelopathic response index (RI) and Synthesis effect (SE)

The negative values of RIs recorded in this study indicated that the growth characteristics of lentil crop were adversely impacted by the different doses of the PLB (Table 4). The synthesis effect (SE) values also indicated significant growth inhibitory impact of weed PLB on lentil crop which was more pronounced at higher doses (Fig. 4).

Table 4

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on the allelopathic index (RI) of lentil (*Lens culinaris*). Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). RI values with same letter in the same columns indicate that they do not differ from each other by means of ANOVA compared to the Duncan test at 0.05 probability level.

Treatments	Germination percentage	Shoot length (cm)	Root length (cm)	Shoot biomass (g)	Root biomass (g)	Number of pod/plant	Number of seed/plant	Pod biomass (g)	Seed biomass (g)	Total biomass (g)
H1	-0.05 a	-0.08 a	-0.24 a	-0.29 a	-0.07 a	-0.26 a	-0.28 a	-0.30 a	-0.33 a	-0.28 a
H2	-0.13 b	-0.11 a	-0.25 a	-0.34 a	-0.18 ab	-0.44 ab	-0.43 a	-0.50 b	-0.54 b	-0.41 b
H4	-0.20 c	-0.14 ab	-0.26 a	-0.41 a	-0.42 bc	-0.47 ab	-0.49 ab	-0.59 b	-0.64 bc	-0.51 b
H8	-0.38 d	-0.24 b	-0.36 b	-0.54 b	-0.57 c	-0.64 b	-0.69 b	-0.78 c	-0.79 c	-0.67 c

Impact on soil characteristics

After crop harvesting, the soils amended with different doses of PLB showed significant enhancement of soil conductivity (11–322%), total organic carbon (10–145%) and total nitrogen (100–400%) ($p < 0.01$) with increasing doses of PLB (Table 5). In contrast, the soil pH (0.23–6%) and available phosphorus (8–25%) declined significantly ($p < 0.01$) with the increasing PLB doses. Inter-dose differences also tended to be significantly different.

Table 5

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on soil properties after crop harvesting. Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). Mean values with same letter in the same columns indicate that they do not differ from each other by means of ANOVA compared to the Duncan test at 0.05 probability level.

Treatments	pH (Mean ± S.E.)	Conductivity (mS) (Mean ± S.E.)	Total nitrogen (%) (Mean ± S.E.)	Organic carbon (%) (Mean ± S.E.)	Available phosphorous (mg/g) (Mean ± S.E.)	Total phenolic contents (mg/g dry weight) (Mean ± S.E.)
H0 (Control)	8.62 ± 0.01 a	0.09 ± 0.003 d	0.01 ± 0.001 e	0.40 ± 0.003 d	0.12 ± 0.002 a	0.33 ± 0.005 e
H1	8.60 ± 0.01 a	0.10 ± 0.005 d	0.02 ± 0.001 d	0.44 ± 0.01 c	0.11 ± 0.001 b	0.91 ± 0.01 d
H2	8.52 ± 0.01 b	0.12 ± 0.004 c	0.03 ± 0.002 c	0.45 ± 0.01 c	0.11 ± 0.001 c	1.19 ± 0.01 c
H4	8.32 ± 0.01 c	0.17 ± 0.005 b	0.04 ± 0.001 b	0.48 ± 0.01 b	0.10 ± 0.001 d	1.37 ± 0.01 b
H8	8.12 ± 0.01 d	0.38 ± 0.005 a	0.05 ± 0.001 a	0.98 ± 0.01 a	0.09 ± 0.001 e	1.69 ± 0.004 a

The phenolic content of PLB-treated soils increased (175–412%) significantly ($p < 0.001$) with increasing doses of applied PLB. The mean value of the phenolic content of unamended soil (control) was significantly ($p < 0.05$) lower compared to the phenolic content recorded in soils amended with different PLB doses. This phenolic content in amended soils increased with increasing doses of PLB applied (H1-H8).

Identification of potential allelochemicals

A total of 35 compounds were identified from the leaf of the invasive weed *Hyptis* that accounted for 99.97% of the compounds in the methanolic extract (Table 6). They were mainly alkaloids (41.35%), fatty acid (18.48%), alkane (15.69%), terpenes (14.47%), phenolics (2.91%) and others (7.07%). Among these 35 compounds, the highest relative content was presented by Ethyl iso-allocholate (30.56%), followed by Tetratetracontane (14.38%), 9,12,15-Octadecatrienoic acid,2,3-bis[(trimethylsilyl)oxy]propyl ester,(Z,Z,Z) (11.09%), Cholest-22-ene-21-ol,3,5-dehydro-6-methoxy-pivalate (4.85%), 11alpha-Hydroxyprogesterone (3.21%), Squalene (3.18%), Dehydroabietinol (3.05%), Dibutyl phthalate (2.82%), 1-Heptatriacotanol (2.33%), Phenol,2-methoxy-3-(2-propenyl) (2.13%) and Dihydroartemisinin,6-deshydro-5-deshydroxy-3-desoxy (2.09%).

Table 6

Compounds in methanolic leaf extract of the invasive- weed *Hyptis suaveolens* (L.) Poit. that were identified by GC-MS.

S.No.	Retention time	Compound name	Percentage of Compound
1	7.28	Phenol, 2-methoxy-3-(2-propenyl)	2.13
2	7.63	4-Allyl-2-methoxyphenyl 2-methylbutyrate	0.29
3	8.07	Caryophyllene	0.3
4	10	7-Heptadecene, 1-chloro	0.44
5	10.08	Caryophyllene oxide	0.73
6	12.25	10-Heneicosene (c,t)	0.25
7	12.32	Eicosane	0.37
8	12.72	3,7,11,15-Tetramethyl-2-hexadecen-1-ol	1.24
9	12.97	Phthalic acid, 2-cyclohexylethyl isobutyl ester	0.28
10	13.52	7,9-Di-tert-butyl-1-oxaspiro(4,5)deca-6,9-diene-2,8-dione	0.49
11	13.62	Hexadecanoic acid, methyl ester	0.99
12	13.96	Dibutyl phthalate	2.82
13	14.36	Octadecane, 3-ethyl-5-(2-ethylbutyl)	0.94
14	14.54	Ethyl iso-allocholate	30.56
15	15.1	7-Isopropyl-1,1,4a-trimethyl-1,2,3,4,4a,9,10,10a-octahydrophenanthrene	0.73
16	15.26	Methyl linoleate	1.19
17	15.31	trans-13-Octadecenoic acid, methyl ester	1.92
18	15.46	Phytol	0.85
19	15.56	Heptadecanoic acid, 16-methyl-, methyl ester	0.47
20	16.23	Cholest-22-ene-21-ol, 3,5-dehydro-6-methoxy-pivalate	4.85
21	17.41	1-Heptatriacotanol	2.33
22	17.93	Dehydroabietinol	3.05
23	18.91	Benzenepropanoic acid, 4-[(2,4-dinitrophenyl)azo]-methyl ester	1.15
24	19.04	Perhydroindene-4-carboxylic acid, 6-acetoxy-2,3-epoxy-1,1-epoxymethyl-3a-hydroxy-5-isopropenyl-7a-methyl-7-oxo-, methyl ester	1.39
25	20.22	Tetratetracontane	14.38
26	20.48	9,12,15-Octadecatrienoic acid, 2,3-bis[(trimethylsilyl)oxy]propyl ester, (Z,Z,Z)	11.09
27	21.07	Dihydroartemisinin, 6-deshydro-5-deshydroxy-3-desoxy	2.09
28	21.76	Squalene	3.18
29	22.51	11alpha-Hydroxyprogesterone	3.21
30	22.61	Benz[e]azulene-3,8-dione, 3a,4,6a,7,9,10,10a,10b-octahydro-3a,10a-dihydroxy-5-(hydroxymethyl)-7-(1-hydroxy-1-methylethyl)-2,10-dimethyl-, [3aR-(3aà,6aà,7à,10á,10aá,10bá)]	1.55
31	22.71	4-(2-Acetyl-5,5-dimethylcyclopent-2-enylidene)but an-2-one	1.68
32	22.77	2-Propenal, 3-(2,6,6-trimethyl-1-cyclohexen-1-yl)	1.23
33	23.12	Dihydroxanthin	0.53
34	23.21	1-Monolinoleoylglycerol trimethylsilyl ether	0.64

S.No.	Retention time	Compound name	Percentage of Compound
35	23.33	7,8-Epoxyloganostan-11-ol, 3-acetoxy	0.63

Discussion

Allelopathic interaction can be considered as a chemical-mediated interference of one species with the growth of other species (Rice 1984). Allelochemicals are basically secondary metabolites released by plants as by-products of primary metabolic processes, and their major role is to protect the plants from abiotic stress (Latif et al. 2017). Our study attempted to understand the allelopathic influence of rapidly advancing invasive weed *Hyptis suaveolens* that enabled its invasibility. The study revealed that the seed germination and growth of leguminous crop lentil was adversely impacted by the soils amended with PLB of this invasive weed that entered the soil system on its decomposition in the field. The adverse impact increased with increasing applied dose of the PLB, indicating the increasing amount of allelochemicals released from the higher doses of PLB. These allelochemicals, as recorded from GC-MS investigation of the methanolic leaf extract of this weed, could be derivatives of phenolic, terpenes, fatty acid, alkaloids etc. Li et al. (2019) opined that such derived compounds have been reported to have growth inhibitory effect on several crop species. In fact, the incomplete removal of weed-biomass in the fields has been reported to adversely impact the succeeding crop yield (Chikoye et al. 2000; Gupta and Narayan 2010).

The invasive weeds could be considered influencing the adjoining plant communities by altering the soil characteristics. This study showed that the PLB of this weed enhanced the soil fertility, as evinced by investigation on organic carbon and total nitrogen. This should have enhanced the crop growth. But in contrast, crop growth declined in soils amended with PLB of this weed which could be attributed to some other factors e.g. increasing secondary metabolites like phenolic content in soil that had an overriding retardatory influence on crop growth and yield. The quality and scale of weed impact was, however, dose-dependent. Lentil seed germination was adversely impacted at higher doses of PLB. However, this adverse impact was not significant at lower dose ($< 2\text{ g kg}^{-1}$ soil), indicative of higher dose-dependent influence at germination stage. Such an inhibitory impact by this weed's leaf extract has been reported on seed germination of other crops e.g. *Oryza sativa* by Oraon and Mondal (2021). In fact, the germination of plant seeds constitutes a primary step towards the growth and development of many plant species, thus, the result in the present study, highlights the importance of allelopathic activity (Gorai et al. 2014; Wang et al. 2019; Hussain et al. 2020b). This inhibitory impact on seed germination may be due to the release of different allelochemical constituents on decomposition of leaf-biomass of the weed, which was often too slow to affect germination during the short period for crop emergence. These allelochemicals may be released from plants by several ways including volatilization, leachate, residue degradation, and root exudation too (Hernandez-Aro et al. 2016; Latif et al. 2017; Mehmood et al. 2018; Laxman et al. 2019; Ghimire et al. 2020; Zhang et al. 2020).

The lentil growth and its yield significantly declined with increasing dose (H1-H8) of *Hyptis* PLB added to the soil. Similar results were also observed on the crop growth by the application of leaf-biomass and leachate of several other invasive weeds in laboratory experiments (Siyar et al. 2018; Laxman et al. 2019; Lal et al. 2021). Such an allelopathic activity depends on the concentration of allelochemicals which generally varies with species (Bari and Kato-Noguchi 2017). Sharma et al. (2019) reported the presence of various chemical compounds in the leaves of this exotic weed *Hyptis suaveolens* which had growth retardatory impact on rice growth. Aromatic plants of Lamiaceae to which the investigated weed belonged, has been found to exhibit phytotoxicity, inhibiting germination and seedling growth (de Almedia et al. 2010; Pinheiro et al. 2015). Another weed *Salvia plebeia* of Lamiaceae has also been reported to have inhibitory impact on crop seed germination, biomass and chlorophyll contents (Husna et al. 2016).

In the present study, besides allelopathic effect on growth characteristics (shoot and root length and their respective biomass) (Table 2), a significant reduction in the photosynthetic chlorophylls (a, b and total) and carotenoids (Fig. 2) and protein content (Fig. 3a) were also recorded in the leaves of the test crop plants. Batish et al. (2007b) observed the similar decline in chlorophyll content of legume crops when grown in soils amended with leaf-residue of *Chenopodium murale* L. (annual weed). This decline in photosynthetic pigments may be attributed to either decreased synthesis of chlorophyll or its enhanced degradation or both (Yang et al. 2004; Desai and Gaikwad 2015). Terpene-derivative chemical constituents can also reduce the amount of photosynthetic pigments in the leaves of recipient crop (Kordali et al. 2007; Kaur et al. 2010; Sharma et al. 2019). Chlorophyll and carotenoids constitute the central part of the energy manifestation of evergreen plant system and therefore, any significant alteration in their levels is likely to have a marked effect on the photosynthetic metabolism of the plant (Sun et al. 2017). Protein plays a vital role in biological processes as it regulates growth, development and reproduction of plants (Duke and Dayan 2006; Maiti et al. 2013). In the present study, it decreased significantly with increasing dose of PLB of the investigated weed. The level of protein as well as amino acids has been reported to be reduced under allelopathic impact El-Shora

et al. (2022). Protein degradation suppress the absorption as well as transportation of amino acids that results in interrupted protein synthesis (Ghayal et al. 2011; Thapar 2012; Huang et al. 2013; Lee et al. 2016). The allelochemicals (mainly phenolic compounds) get accumulated in the plant cell and may interfere with the cytoplasmic ribosomes, and RNA formation, which results in low protein synthesis (Hegab and Ghareib 2010).

In contrast to the observed growth retardatory impacts on the lentil plants with increasing dose of PLB, a significant stimulatory impact on proline and phenolic content was evinced in the present investigation (Fig. 3b, c). Proline, considered as a stress marker, an amino acid, is a solute that enhances tolerance, and is reported to protect against a variety of abiotic stresses (Flores et al. 1988). Increase in proline accumulation with increasing dose of weed-PLB in contrast to significant trend of reduction in the photosynthetic pigments and protein contents, indicates enhanced production of proline under stress-generated conditions (e.g. decline in synthesis of photo-pigments, protein degradation etc.) through the allelochemicals released by the investigated invasive weed *Hyptis suaveolens* on decomposition. El-Shora et al. (2022) reported that phenolic content increased in recipient plant after applying leaf extract of donor invasive (*Rumex dentatus*) plant. It is generally believed that allelochemicals enhance the content of non-enzymatic antioxidants (Garcia-Sanchez et al. 2012) like phenolics (Vinson et al. 2001). The antioxidant property of phenolic compounds has been proposed because of several mechanisms that include up-regulation of antioxidant defense, scavenging reactive oxygen species (ROS) and its formation (Dai and Mumper 2010; Swietek et al. 2019).

In this study, the allelopathic response indices (RI) were less than zero, indicate that the varying doses of applied PLB inhibited the different growth characteristics of lentil plants. The allelopathy inhibition effect increased with increasing doses of applied PLB. According to synthetical effect (SE) and their value, it is evident that varying doses of PLB inhibited the growth of lentil crop in dose dependent manner ($H1 > H2 > H4 > H8$). Similar dose dependent effect of weed on crops has been observed by Balah et al. (2022) and Dai et al. (2022).

In the present study, no negative impact of applied PLB doses of invasive weed *Hyptis suaveolens* was observed on soil resource status at least upto about three months after its incorporation in the soils. On the other hand, the applied weed-PLB into the soil in this period improved the nutrients (organic carbon and total nitrogen) (Table 5). In fact, decomposing residues of invasive species enhance soil nutrients, which are often utilized for their own propagation (Sharma et al. 2017; Kaur et al. 2019). Enhanced electrical conductivity of the amended soils also indicates greater nutrient availability. In contrast, incorporation of PLB into the soil lowered the soil pH in comparison to unamended soils. Similar alteration in soil characteristics (soil pH and electrical conductivity) has been reported by Batish et al. (2009) in soils amended with leaf debris of invasive alien weed *Ageratum conyzoides*. The decline in soil pH is obvious because the phenolics (that increased with increasing doses of PLB of the weed in the current investigation) make the soil acidic (Dalton et al. 1983).

It is well recognised that some weeds adversely influence the growth of neighbouring plant by releasing allelochemicals (Qasem and Foy 2001) that could typically be water-soluble and released by leaching or by microbial decomposition (Singh et al. 2005; Callaway et al. 2008). The most prevalent and extensive water-soluble allelochemicals are generally phenolics (Singh et al. 2005; Szwed et al. 2020). It is suggested that when phenols reach the dynamic soil system, they undergo a range of chemical changes, including microbial activity and adsorption onto organic matter or clay particles (Blum et al. 1999). The allelopathic effect of applied PLB on the crop lentil recorded in the present study could be attributed to the higher amount of the phenolic content as recorded in PLB amended soils. Phenolics may decrease the chlorophyll content and net photosynthetic rate (Lu et al. 2018). Phenolics have also been reported to slow down the plant development by partially inhibiting the nutrient uptake (Baziramakenga et al. 1995; Lehman and Blum 1999). Phenolics have been reported to enhance the activity of indole acetic acid (IAA) oxidase and slow down the reaction of peroxidase (POD) with IAA, bound gibberellin (GA) or IAA that affects the level of endogenous hormones (Cheng and Cheng, 2015). Such growth inhibitory impacts due to increasing levels of phenolics has been reported on other crop plants by several workers e.g. Batish et al. (2007a), Zhang et al. (2012).

The applied PLB in the present study exhibited improvement in soil nutrient status. In contrast, this study also exhibited adverse impact on the growth of associated plants ostensibly through biochemical impact of allelochemicals. These allelochemicals may adversely impact plant processes such as hormonal balance, protein synthesis, respiration, photosynthesis, chlorophyll formation and plant water relations (Fagodia et al. 2017; Mahdavia et al. 2017; Kumar et al. 2020; Yousefi et al. 2020; Khaleghnezhad et al. 2021). This is intelligible from the GC-MS analysis that revealed presence of 35 distinct chemical compounds in the methanolic leaf extract of *H. suaveolens* that majorly belonged to different classes of alkaloids (41.35%), fatty acid (18.48%), alkane (15.69%), terpenes (14.47%), phenolic (2.91%) compounds, which are considered as allelopathically important phytochemicals that inhibited the growth of several crop species (Li et al. 2019; de Oliveira et al., 2021). Lomas et al. (2022) identified forty-one functional groups of different classes of compounds in the same investigated weed *Hyptis*, of which 71% were reported from its leaf organ alone, implying a significant role of leaf harboring the allelochemical potentials. Alkaloid compounds (highest percentage in present study) may retard the crop growth by affecting the DNA

synthesis, respiration and electron transport (Hagan et al. 2013). Among the identified 35 chemical compounds present in *H. suaveolens*, squalene and caryophyllene oxide have been reported to have allelopathic impact on the growth of plants (Flores-Palacios et al. 2015; Abd El-Gawad 2016; Abd El-Gawad et al. 2019). Compound dibutyl phthalate has certain allelotoxicity to tobacco seedlings and the growth of *Microcystis aeruginosa* (Jiajun et al. 2017; Gu et al. 2017). Compound 2-hexadecen-1-ol, 3,7,11,15-tetra-methyl is a decomposition product of chlorophyll and is cytotoxic (Kumar et al. 2010). Several identified compounds (Caryophyllene; 10-Heneicosene (c,t); Eicosane; Hexadecanoic acid, methyl ester; Phytol; Cholest-22-ene-21-ol, 3,5-dehydro-6-methoxy-pivalate; Tetratetracontane etc.) showed different biological activities like antibacterial, antifungal, antimicrobial and antioxidant (Sharma and Cannoo 2016; Frank et al. 2016; Selvaraju et al. 2021; Subin et al. 2021; Albratty et al. 2021; Adelusi et al. 2022). The compound ethyl- iso-allochololate is used in medical research (Thakur and Ahirwar 2019).

Accordingly, several researchers have opined that various phenolic derivatives (Bhuiyan et al. 2010; Ghayal et al. 2011; Huang et al. 2013; Narendhran et al. 2014) and terpene derivatives (Eshilokun et al. 2005; Conti et al. 2012; Ashitani et al. 2015; Bezerra et al. 2017; Sharma et al. 2019) allelochemicals present in leaf part of the investigated weed *Hyptis suaveolens* may significantly impact the adverse growth of associated plants including the crops. Thus, the currently observed decline in crop growth in soils amended with different doses of PLB should rather result from allelochemicals released into the soil from the applied PLB. These results depicted stimulatory impact on soil nutrients (organic carbon and total nitrogen) with increasing dose of PLB in contrast to declining total biomass (upto 67% biomass loss at 8g/kg soil) of the crop in this study. It is opined by some workers that allelochemicals may kill different soil microorganisms, and upon decomposition such microorganism may enhance the soil nutrients (Rice 1984; Rizvi and Rizvi 1992). On the whole, invasibility of the weed *Hyptis suaveolens* in the newly invaded areas in Indian dry tropics, despite improving soil fertility, appears validated due to its ability to inhibit the crop seed germination and growth by adversely impacting synthesis of photo-pigments and proteins through release of allelochemicals and concomitant induction of proline and phenolics under physiologically stressed conditions (Sharma et al. 2019; Sharma and Raghubanshi 2007; Li et al. 2006; Fan et al. 2010). The results of present investigation also demonstrated that the impact of allelopathy is dose dependent. Similar observations were reported in *Ageratina adenophora* (Yang et al. 2016), *Chromolaena odorata* (Laxman et al. 2019), *Paspalum commersonii* (Zaman et al. 2018) and *Solanum elaeagnifolium* (Balah et al. 2022).

Conclusions

In conclusion, the powdered leaf-biomass of the invasive weed *Hyptis suaveolens*, despite adding to the fertility of soil initially, adversely impacts seed germination and growth of lentil crop through allelopathy, although these allelopathic effects are dose dependent. Besides, inhibitory effect on lentil crop, GC-MS analysis in present study indicates the existence of various allelochemicals like alkaloids, phenolics etc. in its leaves which probably get released in the soil system after leaf-residue decomposition and alter the soil characteristics. These allelochemicals reduce the synthesis of photosynthetic pigments, proteins and ultimately crop growth. Thus, that invasive weed *Hyptis suaveolens* uses its allelochemicals as weapons to replace the native vegetation in its invaded range and in consequence may be successful invader in dry tropical urban regions. Further research is required to understand its allelopathic behaviour under natural field conditions like release of various phytotoxic allelochemicals in the soil, resultant changes in soil chemistry and the length of persistence of these allelochemicals in soil system.

Declarations

Conflict of interest

There are no conflicts of interest.

Author contribution statement

Maneesh Kumar Lomas and Ms. Anjali carried out the work jointly as research scholars, designing the experiment and various biochemical analyses under the supervision of Prof. Rup Narayan. Maneesh Kumar Lomas performed statistical analyses with the contribution of Dr. Shachi Agrawal. The manuscript was drafted by Prof. Rup Narayan. All authors read and approved the final manuscript.

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Figures

Figure 1.

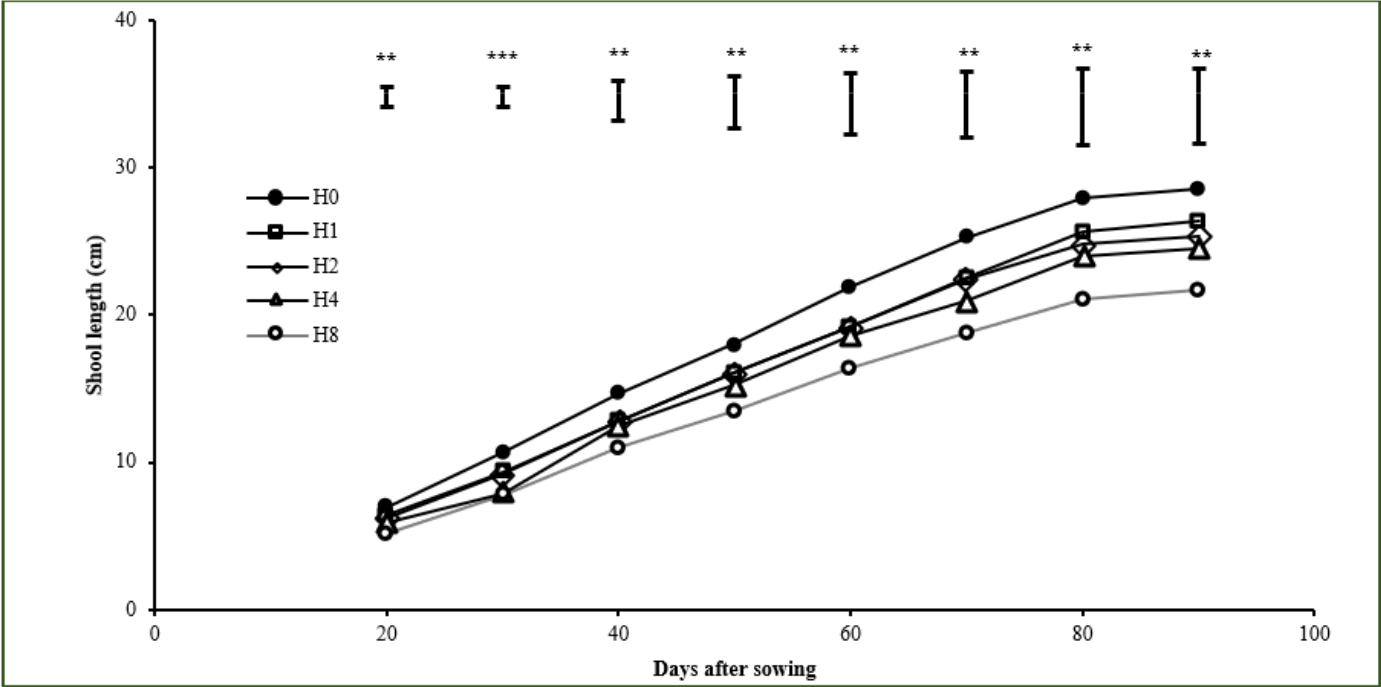


Figure 1

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on the shoot length of lentil (*Lens culinaris*) at different growth stage. Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). Bars indicates the LSD between treatment mean (df=55). ** indicates significant at the level of $p < 0.01$ and *** $p < 0.001$.

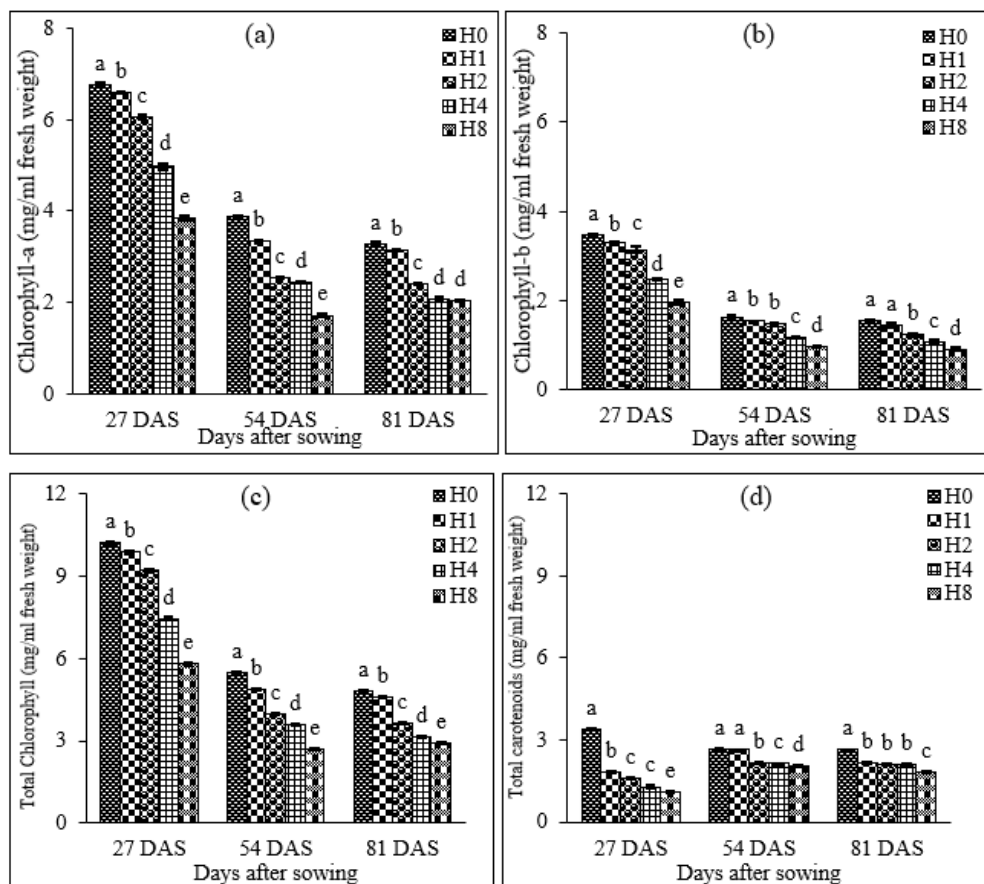


Figure 2

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on the photosynthetic pigments of lentil (*Lens culinaris*) at different growth stage. Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). Same letter over the bars indicate that they do not differ from each other by means of ANOVA compared to the Duncan test at 0.05 probability level.

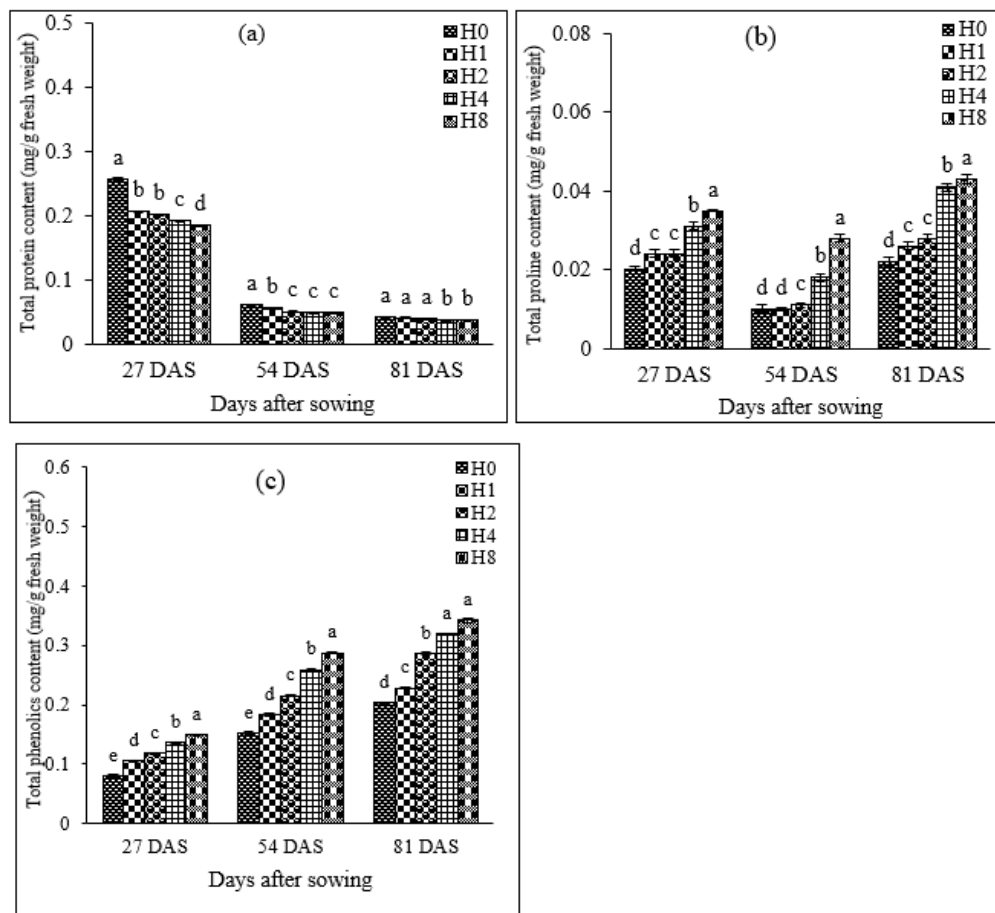


Figure 3

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on biochemical attributes (Total protein, total proline and total phenolic content) of lentil (*Lens culinaris*) at different growth stage. Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). Same letter over the bars indicate that they do not differ from each other by means of ANOVA compared to the Duncan test at 0.05 probability level.

Figure 4.

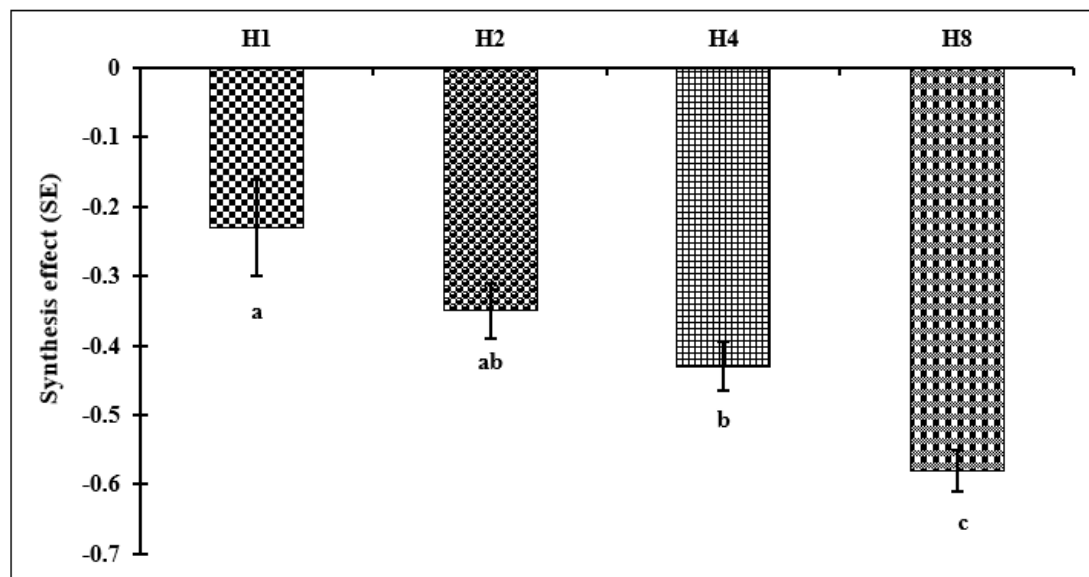


Figure 4

Impact of applied powdered leaf-biomass (PLB) doses of the invasive weed *Hyptis suaveolens* L. (Poit.) on the synthesis effect (SE) of lentil (*Lens culinaris*). Digits (1, 2, 4, 8) suffixed to species code (H) indicate weight of PLB incorporated (g/kg soil). Same letter over the bar do not differ from each other by means of ANOVA compared to the Duncan test at 0.05 probability level.