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Bridging the gap: linking morpho-functional traits' plasticity with hyperaccumulation

**Padma Sharma · Mustaqeem Ahmad ·
Sonia Rathee · Harminder P. Singh** (ORCID) ·
Daizy R. Batish · Ravinder Kumar Kohli

Abstract Plant species exhibiting heavy metal tolerance are instrumental in phytoremediation of metalliferous sites. Most of the time, variations in plant functional traits (PFTs) are overlooked while identifying hyperaccumulators. However, investigating morphological, physiological, and phenological variations can contribute to our knowledge about stress tolerance, and aid in identifying potential hyperaccumulators. In the present study, we investigated variation in morpho-functional traits in *Solanum nigrum,* a known hyperaccumulator, under lead (Pb) stress. Twenty-one PFTs including 9 above-ground (leaf count, leaf area, specific leaf area, leaf dry matter content, leaf thickness, leaf dry mass, shoot length, stem dry mass, stem diameter), 3 below-ground (root length, root dry mass, and root diameter), 4 reproductive (flower bud count, fruit count, flower count, and fruit dry mass), and 5 photosynthetic traits (total chlorophyll, total carotenoid, chlorophyll *a*, chlorophyll *b*, and photosynthetic efficiency) under varying Pb concentrations (500–2000 mg kg^{-1}) were assessed. Pillai's trace test (MANOVA) depicted significant variations in above-ground, below-ground, and photosynthetic traits, whereas reproductive traits did not vary significantly with progressive metal concentration. However, most of the studied traits except flower count, fruit dry mass, and chlorophyll *b* varied significantly under Pb stress. The study depicts that enhanced PFT's plasticity enables *S. nigrum* to grow in Pb-contaminated soil effectively without impacting plant fitness. Plasticity of morpho-functional traits, therefore, establishes itself as a resourceful approach in successful identification of phytoremediation capacity of a plant.

Keywords Tolerant species · Non-biodegradable pollutant · Morphological attributes · Pb contamination · Plant functional traits

P. Sharma · M. Ahmad · H. P. Singh (✉)
Department of Environment Studies, Panjab University, Chandigarh 160 014, India
e-mail: hpsingh_01@yahoo.com

S. Rathee · D. R. Batish (✉) · R. K. Kohli
Department of Botany, Panjab University, Chandigarh, India
e-mail: daizybatish@yahoo.com

Introduction

Heavy metals (HMs) infiltrate the soil environment through diverse sources such as foundries, mines, smelters, combustion of fossil fuel, agriculture, and industrial effluents (Masood et al., 2021; Yan et al., 2020). These are inherently non-essential and are conventionally known for their toxicity, persistence in nature, and bioaccumulative property (Ali et al., 2019). HMs also affect human and animal health through malfunctioning of nerves, kidneys, muscles, etc. (Saher & Kanwal, 2019). In plants, HMs induce inactivation of enzymes, production of cytotoxic compounds

(reactive oxygen species, ROS such as hydrogen peroxide, H_2O_2; hydroxyl radical, OH; superoxide radical, $O_2^{\bullet-}$), DNA fragmentation, denaturation of proteins, and alteration of major metabolic processes such as respiration, photosynthesis, and homeostasis, and disruption of oxidative metabolism (Ghori et al., 2019).

Lead (Pb), the 2nd most toxic metal, is a widely present inorganic pollutant encompassing 0.002% of the Earth's crust (Zulfiqar et al., 2019). Pb toxicity is a matter of global concern since it impacts all ecological spheres through various anthropogenic activities and pedogenic processes (Pourrut et al., 2011). Although Pb accumulation plays no crucial role in plant physiology, yet the evidence of alteration in various metabolic processes and ultrastructure changes in plants has been reported (Ghori et al., 2019; Kaur et al., 2013, 2014; Zulfiqar et al., 2019). Pb mobilization results in deleterious effect on growth, development and productivity of plants, and composition and structure of soil microbial communities (Pourrut et al., 2011; Zulfiqar et al., 2019). Pb toxicity is species-specific, dependent upon Pb concentration, plant developmental stages, and the period of metal exposure (Gul et al., 2020).

Phenotypic plasticity in plants is predominantly concerned with morphological (leaves, flower, bud, and stem traits), physiological (physiological integration, division of labor), phenological and ecological plasticity of individual species (Xu & Zhou, 2016). As HMs affect the biochemistry and physiology of a plant (Ghori et al., 2019), the resultant alteration can also be witnessed in plant functional traits (PFTs) (Song et al., 2019). Previously, a few studies have demonstrated that HMs induce morpho-functional variations in the plants, which enable the plant to thrive under metal-stressed environments. For example, HMs like Cd, Cu, and Zn induced adaptive plasticity in physiological processes in peanut (Shi & Cai, 2009). Chen et al. (2015) reported that successful colonization of *Phytolacca americana* in Mn-contaminated soil was related to phenotypic plasticity. Likewise, morpho-functional traits in *Leptodictyum riparium* changed with metal concentration and provided insights into tolerance mechanism (Maresca et al., 2018).

Plants growing in metalliferous soil either prevent the entry of HMs into the cellular cytoplasm (avoiders) or detoxify metal ions crossing the cell membrane (tolerant) (Millaleo et al., 2010). Accordingly, plants are classified as metal excluders, indicators, and hyperaccumulators. Hyperaccumulators/tolerant plants are instrumental in phytoremediation of metalliferous sites (Saad-Allah & Elhaak, 2017; Suman et al., 2018). In hyperaccumulators, antioxidant machinery has been recognized as instrumental in tolerance, but till date, it has not been dwelled in deep how PFTs vary in hyperaccumulators. Most of the time, variations in PFTs are generally overlooked; if studied, they can help in improving the knowledge about stress tolerance mechanism and identification of potential hyperaccumulators, which can be further used in phytomining. Since detecting morpho-functional plasticity is an effective solar-driven and cost-effective approach, it should serve as an alternative indicator of metal hyperaccumulation. Therefore, we hypothesized that variations in PFTs enable the plant to cope up with metal stress and sustain fitness in HM-enriched environment. To prove our hypothesis, we chose *Solanum nigrum* L. (family Solanaceae), a well-known hyperaccumulator of Cd, Zn, Pb, Cd, and Ni (Saad-Allah & Elhaak, 2017), as a model plant to study the PFTs' variation under Pb toxicity. To the best of our knowledge, such type of work has not been undertaken previously. In the present study, we analyzed 21 functional traits: nine above-ground (leaf count, leaf area, specific leaf area, leaf dry matter content, leaf thickness, leaf dry mass, shoot length, stem dry mass, stem diameter), three below-ground (root length, root dry mass, and root diameter), four reproductive (flower bud count, fruit count, flower count, and fruit dry mass), and five photosynthetic traits (total chlorophyll, total carotenoid, chlorophyll *a*, chlorophyll *b*, and photosynthetic efficiency) under varying Pb concentrations (0–2000 mg kg^{-1} soil) for assessing adaptive variations.

Materials and methods

Soil samples and characteristics

The soil samples were collected at a depth of 0–0.2 m from unpolluted sites in Panjab University, Chandigarh, India. The collected soil was air-dried and sieved to remove stones and other debris. After sieving, soil was mixed with manure and sand in the ratio of 3:2:1 (soil:manure:sand) to make the composition

uniform. The soil was spiked with lead nitrate [Pb (NO$_3$)$_2$] at different concentrations of Pb (500, 1000, 1500, 2000 mg kg^{-1}). Thereafter, 200 mg kg^{-1} of ammonium nitrate (NH$_4$NO$_3$) was added to the control soil to normalize the effect of nitrates present in Pb-salt spiked soil. The spiked soil was incubated for 2 weeks for achieving homogenization.

All soil samples were analyzed in triplicates for various soil properties. These were as follows: total nitrogen = 0.69% (Kjeldahl method), total phosphorous = 0.18% (ammonium vanadatemolybbate method], total potassium = 0.52% (ammonium acetate extraction method), and organic carbon = 3.16% (Walkley black method), pH = 6.84 (soil: water = 1:2, *w/v*), and electrical conductivity = 0.60 mmhos cm^{-1} (soil: water = 1:2, *w/v*).

Materials and experiment description

Seeds of *S. nigrum* were collected locally from plants growing in the wild. Seeds were surface sterilized with 10% sodium hypochlorite for 10 min and then rinsed at least 4 times with sterilized deionized water (Jiang et al., 2016). After sterilization, *S. nigrum* seeds were sown in seedling trays filled with substrate soil. Seeds were germinated in a growth chamber at 25 °C, 16/8 h day/night photoperiod, and 70% relative humidity (Fagodia et al., 2017).

Experimental design

The experiment was conducted in 10 cm diameter polyethylene plastic pots of 1 kg capacity. The control and spiked soil with different concentrations were poured into the respective pots. Seedlings having 4–6 true leaves and height of 5–6 cm were randomly selected and transferred to plastic pots filled with 1 kg

soil, with one seedling per pot. There were six replicates of each treatment arranged in a completely randomized design. Distilled water was used for irrigating pots to maintain the soil moisture at 60% during the experimental duration. Plants were grown under natural light and temperature conditions (average day temperature: 18–25 °C; average night temperature: 8–15 °C) in an experimental dome. After 8 weeks, plants were harvested for the measurement and calculation of different parameters. Then, the plants were rinsed with distilled water before subjecting them for the measurement of PFTs.

Analysis of morphological and reproductive traits

Above- and below-ground traits

Root length (cm) and shoot length (cm) were measured with a centimeter scale, whereas leaves were counted manually. Root, shoot, and leaf were separated and subjected to oven drying at 75 °C for 72 h. Root dry mass (RDM; g), stem dry mass (SDM; g), and leaf dry mass (LDM; g) were measured by weighing balance (Mettler Toledo-ME104, 0.0001 g), while leaf thickness (mm), stem diameter (mm), and root diameter (mm) were measured using a digital Vernier caliper (0.1 mm accuracy). For determining specific leaf area (SLA; mm^2 mg^{-1}) and leaf dry matter content (LDMC; mg g^{-1}), the methodology given by Pérez-Harguindeguy et al. (2013) was followed (Table 1). Leaf area (LA; mm^2) was determined using a leaf area meter (CI-202, CID Bio-Science, USA).

Reproductive traits

Flower bud count (per plant), flower count (per plant), and fruit count (per plant) were counted manually,

Table 1 Plant functional traits and how they were calculated

Plant functional traits	Formula	References
Specific leaf area (mm^2 mg^{-1})	$SLA = \frac{One-sided\ area\ of\ fresh\ leaf}{Leaf\ dry\ weight}$	Pérez-Harguindeguy et al., 2013
Leaf dry matter content (mg g^{-1})	$LDMC = \frac{Oven\ dry\ mass\ of\ leaf}{Water\ saturated\ fresh\ mass\ of\ leaf}$	Pérez-Harguindeguy et al., 2013
Chlorophyll a (μg mg^{-1})	$Chla = (10.63 \times A663) - (2.39 \times A645)$	Kaur et al., 2019
Chlorophyll b (μg mg^{-1})	$Chlb = (20.11 \times A645) - (5.18 \times A663)$	Kaur et al., 2019
Total chlorophyll content (μg mg^{-1} d. wt.)	$TChl = (6.45 \times A663) + (17.72 \times A645)$	Arnon (1949)
Total carotenoid content (μg mg^{-1} d. wt.)	$TCaro = (1000 - A_{470} - 3.27 \times Chl\ a - 104 \times Chl\ b)$	Kaur et al., 2019

and fruit dry mass (g) was measured using an electronic weighing balance.

Determination of photosynthetic traits

From each treatment, leaves of the plant were used for determining photosynthetic traits such as photosynthetic efficiency (F_v/F_m), chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll content, and total carotenoid. Among the studied traits, total chlorophyll content and total carotenoid content were estimated according to the method described by Kaur et al. (2019). Chlorophyll was extracted from 25 mg fresh leaves and was incubated in 5 mL of dimethyl sulphoxide (DMSO) at 60 °C for 1 h as per Hiscox and Israelstam (1979). Subsequently, the absorbance of the solution was read on Shimadzu UV-1800 spectrophotometer at 645 nm, 663 nm, and 470 nm taking DMSO as blank. Amounts of Chl a, Chl b, total chlorophyll and total caotenoid were calculated as per equations provided in Table 1. Total chlorophyll and total carotenoid content were expressed on the dry weight basis as suggested by Rani and Kohli (1991). Photosynthetic efficiency was measured by using OS-30p pulse modulated chlorophyll fluorometer (Opti Sciences, USA).

Statistical analysis

The linear model of ANOVA was used to test the effect of treatments on PFTs of *S. nigrum*. Treatments were considered as a fixed factor and PFTs were used as a response variable. On the other hand, PFTs were clustered into qualitative functional groups for multivariate analyses (MANOVA), *viz.,* above-ground (leaves count, leaf thickness, LDM, LA, SLA, LDMC, shoot length, stem diameter, and SDM), below-ground (root length, root diameter, and RDM), reproductive (flower bud count, flower count, fruit count, and fruit dry mass), and photosynthetic traits (photosynthetic efficiency, Chl a, Chl b, total chlorophyll content, and total carotenoid content). Significant effects were evaluated with Tukey's honest significance test for multiple comparisons of group means. All statistical analyses were performed in statistical stats—package

and graphical representation in *ggplot2* package in R version 3.6.0. Every population sample was used for making graphical visualizations. All the differences were tested at $p \leq 0.05$ for determining the statistical significance.

Results

Functional group variation

Multivariate analysis (MANOVA) and Pillai's test (V) was used to test the significance of quantitative groups (group functional traits treated as factor). Above-ground traits ($F = 14.691$, $p < 0.01$), below-ground traits ($F = 17.86$, $p < 0.001$), and photosynthetic traits ($F = 10.1$, $p < 0.01$) varied significantly with treatments, except for reproductive traits ($F = 1.427$, $p = 0.24$) (Table 2).

Above-ground and below-ground trait variations

Above-ground traits such as LA (0.101%) and LDMC (14.89%) decreased (Fig. 1b, d), while leaf count (118.46%), SLA (16.43%), leaf thickness (92.50%), and LDM (294.35%) increased linearly (Fig. 1a, c, e, f). The linear model of ANOVA depicted that all above-ground traits like LA ($F = 1.2737$, $p < 0.001$), LDMC ($F = 2.855$, $p < 0.1$), leaf count ($F = 14.8616$, $p < 0.001$), SLA ($F = 7.6734$, $p < 0.001$), leaf thickness ($F = 47.556$, $p < 0.001$), and LDM ($F = 30.0737$, $p < 0.001$) varied significantly (Table 3). Similarly, shoot length, SDM and stem diameter increased by 160.36%, 379.07%, and 11.81%, respectively (Fig. 1g, h, i). ANOVA showed significant interaction with shoot length ($F = 8.8848$, $p < 0.001$), SDM ($F = 8.8015$, $p < 0.001$), and stem diameter ($F = 6.7092$, $p < 0.01$) (Table 3). In addition, below-ground traits such as RDM (127.37%) and root diameter (56.17%) increased, whereas root length (47.98%) decreased significantly in a linear pattern (Fig. 1k, l, j). A significant interaction was also observed with RDM ($F = 3.0721$, $p < 0.05$), root diameter ($F = 5.8571$, $p < 0.05$), and root length ($F = 4.4438$, $p < 0.05$) (Table 3).
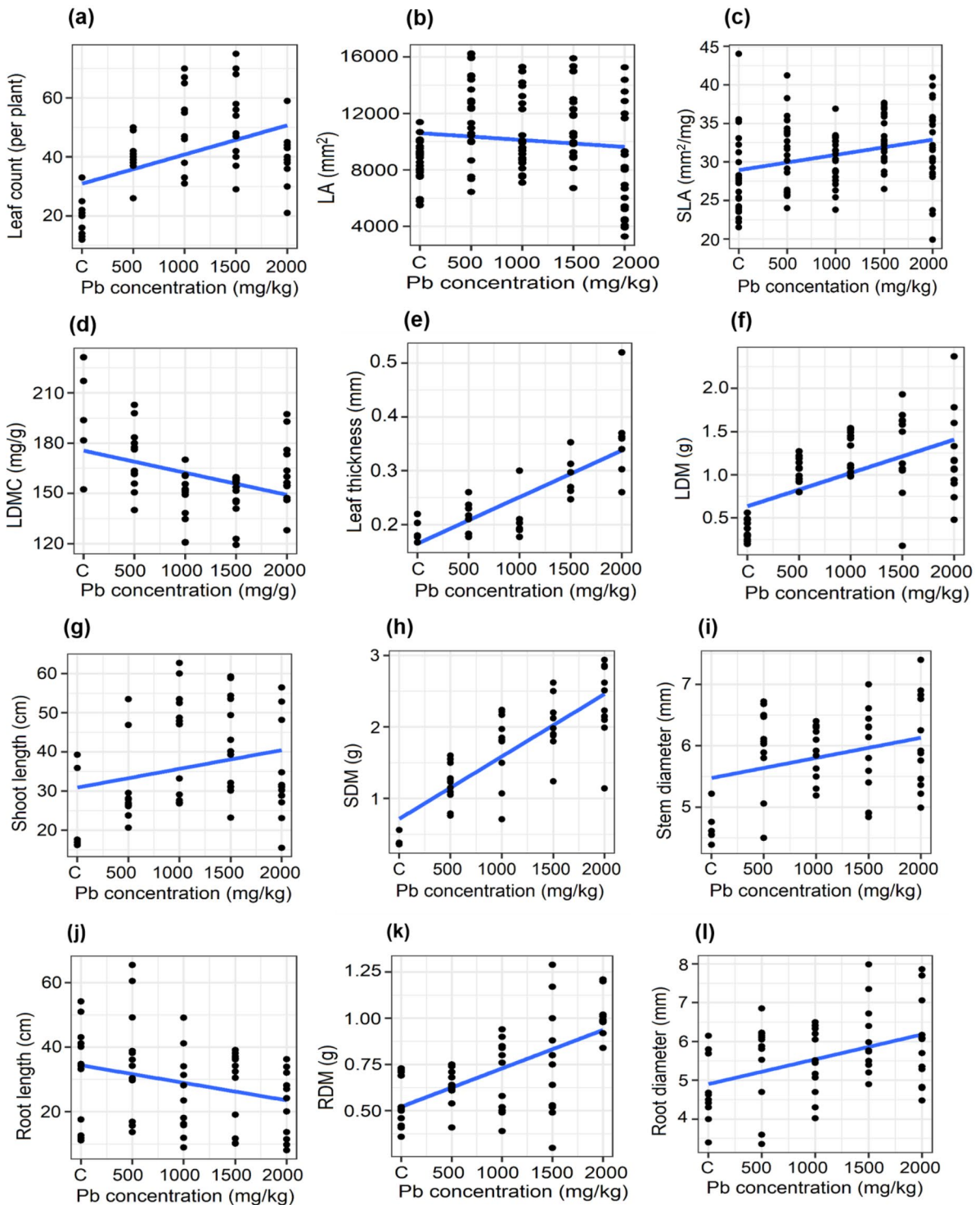
Fig. 1 Fitted linear model regression on above-ground and below-ground traits' variation with different concentrations of Lead (Pb) in *Solanum nigrum. LA: leaf area; SLA: spe-cific leaf area; LDMC: leaf dry matter content; LDM: leaf dry mass; SDM: stem dry mass; RDM: root dry mass*

Table 2 MANOVA to test the functional group variation along with different concentrations (C) of Lead (Pb) in *Solanum nigrum*

Response variables	Factors	Pillai	*F*-value	num Df	den Df	Pr(> *F*)
Above-ground traits	(Intercept)	0.99815	299.411	9	5	< 0.001
	C	0.96356	14.691	9	5	< 0.01
Reproductive traits	(Intercept)	0.91858	135.385	4	48	< 0.001
	C	0.10629	1.427	4	48	**0.24**
Below-ground traits	(Intercept)	0.97829	841.05	3	56	< 0.001
	C	0.489	17.86	3	56	< 0.001
Photosynthetic traits	(Intercept)	0.99973	3663.2	7	7	< 0.001
	C	0.91024	10.1	7	7	< 0.01

Values in Bold are not significant

Reproductive trait variations

The reproductive traits such as flower bud count, flower count, and fruit count linearly increased with increasing Pb concentration by 191.176%, 800%, and 139.34%, respectively (Fig. 2a, b, c). However, FDM decreased linearly (9.72%) with increasing concentration of Pb (Fig. 2d). ANOVA revealed significant interaction with flower bud count ($F = 10.2189$,

$p < 0.001$) and fruit count ($F = 3.6846$, $p < 0.05$), while flower count ($F = 1.6814$, $p = 0.2015$) and FDM (g) ($F = 0.1564$, $p = 0.6942$) were non-significant (Table 3).

Photosynthetic traits variation

Photosynthetic traits varied significantly in response to Pb stress. Significant interaction was observed

Fig. 2 Fitted linear model regression on reproductive traits' variation with different concentrations of Lead (Pb) in *Solanum nigrum*
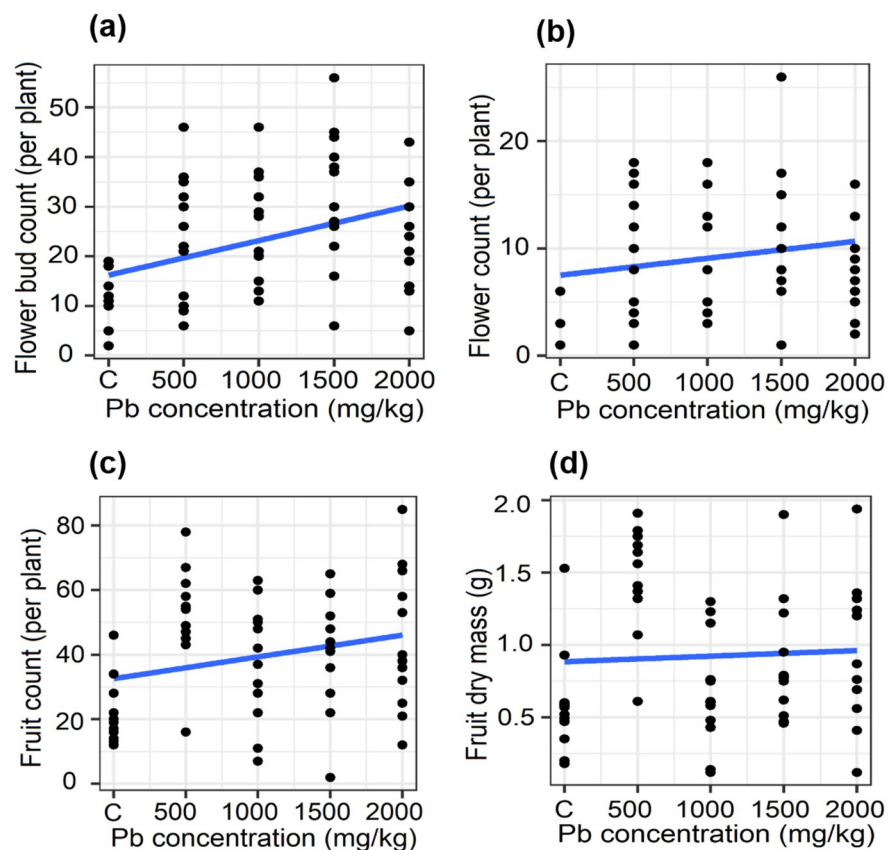
Table 3 ANOVA used to test the effects of different concentrations of Lead (Pb) on measured variables in *Solanum nigrum*

| Response variables	Df	Sum Sq	Mean Sq	F-value	Pr($>F$)
Shoot length (cm)	1	1513.7	1513.72	8.8848	< 0.001
Stem diameter (mm)	1	3.9822	3.9822	6.7092	< 0.01
Stem dry mass (SDM; g)	1	4.4352	4.4352	8.8015	< 0.001
Root length (cm)	1	882.9	882.92	4.4438	< 0.05
Root diameter (mm)	1	9.004	9.0036	5.8571	< 0.05
Root dry mass (RDM; g)	1	0.2067	0.20667	3.0721	< 0.05
Fruit count	1	1360.1	1360.13	3.6846	< 0.05
Flower bud count	1	1456	1456.03	10.2189	< 0.001
Flower count	1	66.1	66.096	1.6814	**0.2015**
Fruit dry mass (FDM; g)	1	0.0445	0.044468	0.1564	**0.6942**
Leaf count	1	2940.3	2940.3	14.8616	< 0.001
Leaf thickness (mm)	1	0.124741	0.124741	47.556	< 0.001
Leaf dry mass (LDM; g)	1	4.4506	4.4506	30.0737	< 0.001
Leaf area (LA; mm^2)	1	12,536,425	12,536,425	1.2737	< 0.001
Specific leaf area (SLA; mm^2/g)	1	290.6	290.552	7.6734	< 0.001
Leaf dry matter content (LDMC; mg/g)	1	271,260	271,260	2.855	< 0.1
Chlorophyll a (µg mg^{-1})	1	94.233	94.233	8.8236	< 0.05
Chlorophyll b (µg mg^{-1})	1	0.7604	0.76043	2.7722	**0.1198**
Total chlorophyll content (µg mg^{-1} d. wt.)	1	150.06	150.055	13.103	< 0.01
Total carotenoid content (µg mg^{-1} d. wt.)	1	3.5217	3.5217	6.1327	< 0.05
Photosynthetic efficiency (F_v/F_m)	1	0.05291	0.05291	17.8652	< 0.001

Values in Bold are not significant

with Chl *a* ($F = 8.8236$, $p < 0.05$), total chlorophyll content ($F = 13.103$, $p < 0.01$), total carotenoid content ($F = 6.1327$, $p < 0.05$), and photosynthetic efficiency ($F = 17.8652$, $p < 0.001$), except for Chl *b* ($F = 2.7722$, $p = 0.1198$) (Table 3). Photosynthetic efficiency (13.42%), Chl *a* (277.92%), total chlorophyll content (224.58%), and total carotenoid content (75.27%) increased linearly with increasing dose of Pb toxicity (Fig. 3a, b, d, e), except for Chl *b* (Fig. 3c) as compared with control (Table 3).

Discussion

In our study, most of the PFTs were found to vary significantly with different Pb concentrations, thereby depicting the potential of *S. nigrum* to exhibit enhanced PFTs in HM-enriched environment. We observed that PFT groups such as above-ground, below-ground, and photosynthetic traits showed highly plastic behavior, while reproductive traits showed the least (Table 3).

Response of above-ground and below-ground traits

Change in growth patterns is a fundamental plant response when encountering biotic and/or abiotic stresses such as heavy metals (Nejat & Mantri, 2017). A slight disturbance in cellular homeostasis triggers an adaptive response in plants. Plant morphology is a parameter utilized for the assessment of plant traits in heterogeneous environments (Abdusalam & Li, 2018). In our results, an increased shoot length and decreased root length were recorded, which might be caused by an uneven distribution of Pb from root to shoot due to an apoplastic and symplastic barrier (Shu et al., 2011). Another reason might be attributed to the phenomenon called hormesis, which is a stimulatory effect in growth reported under the physiologically toxic dose of HMs (Li et al., 2020; Poschenrieder et al., 2013). The observable biomass's increase or decrease is species-specific, dependent on exposure duration to HM and various experimental conditions (soil properties, microflora, fauna, etc.). The increased biomass could be due to Pb-detoxification (Zulfiqar et al., 2019). This might
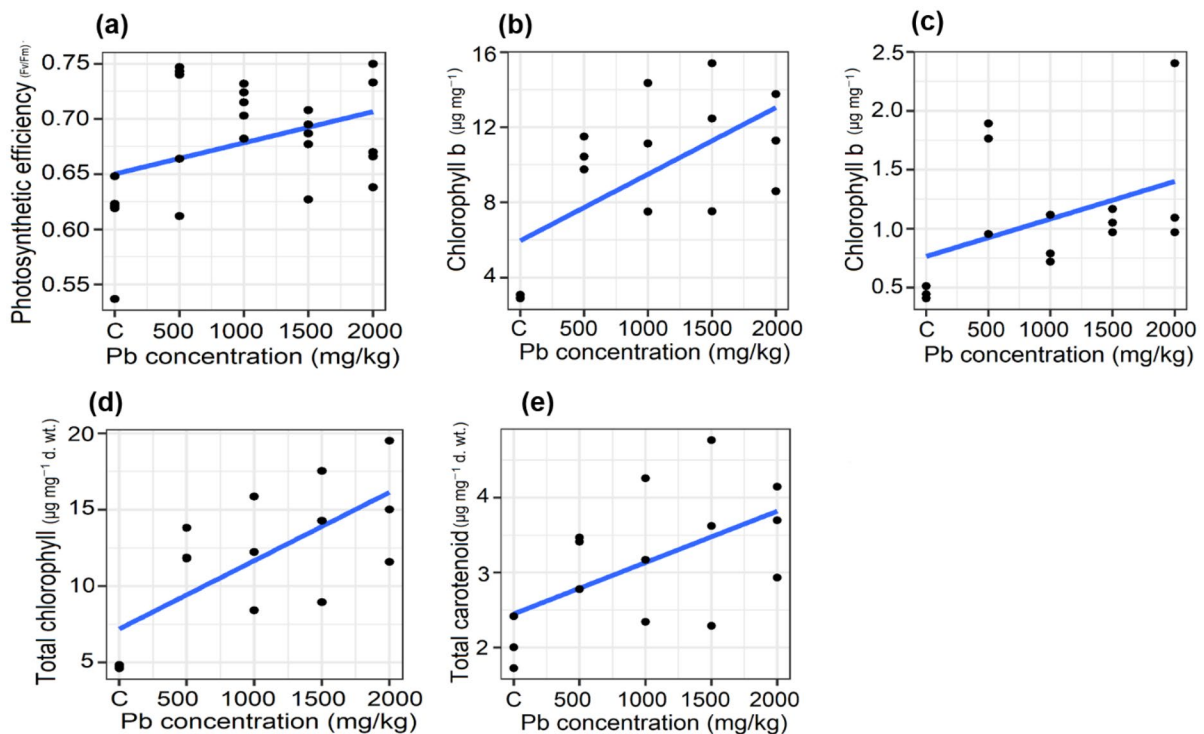
Fig. 3 Fitted linear model regression on photosynthetic traits variation with different concentrations of Lead (Pb) in *Solanum nigrum*

be correlated with the potential to retain Pb in active non-metabolic regions like cell wall and vacuole that facilitate the growth of the plants without any hindrance (Li et al., 2020). Moreover, in our study, there was an increase in root diameter with increasing Pb concentration. It was corroborated by the findings of Zarinkamar et al. (2013) who reported that in *Matricaria chamomilla* at the shooting and flowering stages, root diameter increased as Pb concentration caused thickening of cell walls. Pb stimulated parenchyma cells to rapidly begin the secondary growth, which might be the reason for the increase in root diameter and dry weight of roots with increasing concentration of toxicity (Alle et al., 2019).

Leaves are considered as one of the most important plant part due to their role in light capturing and photosynthesis (Ren et al., 2019; Strauss et al., 2020). The studied leaf morphological traits exhibited significant variations with increasing Pb concentration. Leaf area is often characterized with specific adaptations and is known to be sensitive to drought as well as metal stress conditions (Lopez et al., 2008). Decrease in LA can be attributed to inhibition of cell growth and development of plants following Pb

toxicity (Shu et al., 2011). LDMC is an important parameter for the evaluation of a species resource utilization strategy; thus, variations in LDMC have direct consequences on plant growth (Li et al., 2005).

Moreover, leaf thickness, SLA, leaf count, and LDM depicted a significant increase with increasing concentration of Pb. An increase in leaf thickness generally indicates structural adaptations for water conservation and herbivore defense (Firn et al., 2019). Increased carbon partitioning in leaf area growth enhances SLA and is a key parameter contributing to the morphological plasticity of species (Weraduwage et al., 2015). Higher SLA optimizes resource allocation, thus has a direct bearing on integrated plant growth, reproductive strategies, and lifespan of species (Lin et al., 2020). High SLA is a determinant of low leaf construction cost and represents a trade-off between surface area (for capturing photons) and resource utilization strategies at biogeographical scale (Firn et al., 2019). The morphological parameters like height of the plant, SLA, and LDMC are effective approaches that efficiently reflect the plants' response to changing environmental variables (Yue

et al., 2019). Furthermore, observed enhanced plant growth might also be attributed to protection from pathogenic attack because of growing in a metal-rich environment (Boyd, 2007).

Response of reproductive traits

Reproduction is the most important stage in the life cycle of plant species, which directly affects species performance (O'Brien, 2019). Heavy metal concentration, atmospheric deposition, and plant growth phase are some of the factors which influence metal absorption and accumulation in vegetables and fruits (Lăcătuşu & Lăcătuşu, 2008). As depicted in our results, FDM decreased with increasing Pb dose. Similar results were reported by Elhindi et al. (2018) in *Tagetes erecta* upon treatment with Zn, Co, Mn, and Cu. Our results depicted an increase in flower bud count, fruit count, and flower count, which demonstrates the enhanced reproductive fitness of the plant. An increase in number of flowers in *Streptanthus polygaloides* treated with Ni was recognized as an indication of maintained plant fitness (Jhee et al., 2006). On the contrary, Sankaran and Ebbs (2008) reported that in *Brassica juncea* heavy metal got translocated to seeds but did not exceed the permissible consumption limits. Similarly, Klatte et al. (2009) reported that seeds experienced the least impact of metal toxicity as compared to other parts of plants. Overall, it can be said that an increase in studied reproductive traits might be resultant of reproductive fitness, which helps to maintain progeny fitness in unfavorable environmental conditions.

Response of photosynthetic traits

Chlorophyll content is a crucial indicator of plant photosynthetic efficiency (Haritha et al., 2017). It is usually measured in plants to assess the impact of environmental stress, as changes in pigment contents are linked to visual symptoms of plant illness and photosynthetic productivity (Chandra & Kang, 2016). Pb is non-essential for cell growth and development of plants; however, it is absorbed through roots and sequestered in vacuoles leading to no significant effect on photosynthetic apparatus (Ahmed & Tajmir-Riahi, 1993; Kaur et al., 2014). The observed changes in photosynthetic pigment content may be attributed to the ability of a plant to maintain its growth and fitness by increasing the level of chlorophyll synthesis under Pb-induced stress (MacFarlane & Burchett, 2001). Improved photosynthetic activity enhances the carbon assimilation that results in biomass accumulation for growth sustenance (Simkin et al., 2019). Our results were contrary to the findings of Peng et al. (2020) who revealed that chlorophyll content decreased in *S. nigrum* when treated with Cd. Oladele et al. (2019) observed that chlorophyll content significantly decreased on exposure to Pb and Zn treatments in *Vigna subterranean* and *Zea mays.* The enhanced carotenoid content under increasing Pb concentration further implies their role in ROS quenching, and thus preventing peroxidation of membrane lipids (Ramel et al., 2012). In our study, photosynthetic efficiency increased with a higher dose of Pb, which resulted in enhanced energy conversion and yield (Simkin et al., 2019), and consequently the ability of *S. nigrum* to withstand HM stress and maintain growth fitness.

Conclusions

Conventional tools and technology currently employed are either not cost-effective or are labor-intensive, thereby arose the need for an alternative mode of detecting hyperaccumulator capacity of any plant. The study concludes that *S. nigrum* has the potential to tolerate Pb toxicity through the plasticity of traits as the presence of Pb in contaminated soil enhanced PFTs effectively without impacting plant fitness. Morphofunctional variations, therefore, establishes itself as a resourceful approach in the successful identification of the phytoremediation capacity of a plant. Hence, variations in PFTs provide an additional economical value and help reclamation of HM contaminated soils under field conditions.

Availability of data and materials The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare competing interests.

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