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SHORT RESEARCH AND DISCUSSION ARTICLE

Lonchocarpus cultratus, a Brazilian savanna tree, endures high soil Pb levels

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Abstract

Industrial revolution markedly increased the environmental contamination by different pollutants, which include the metal lead (Pb). The phytoremediation potential of native species from tropical regions is little known, especially for woody plants. The present study aimed to evaluate the performance of *Lonchocarpus cultratus* (Fabaceae), a tree species from the Brazilian savanna, grown in soil that was artificially contaminated with increasing Pb concentrations (control and 4 Pb treatments, 56, 120, 180, and 292 mg kg^{-1}) for 6 months. The biomass of *L. cultratus* was not depressed by exposure to Pb, despite the high accumulation of this metal (up to 7421.23 μg plant^{-1}), indicating a high plant tolerance to this trace metal. Lead was mainly accumulated in roots (from 67 to 99%), suggesting that the low root-to-shoot Pb translocation is a plant strategy to avoid Pb-induced damages in photosynthetic tissues. Accordingly, the content of chlorophylls *a* and *b* was maintained at similar levels between Pb-treated and control plants. Moreover, increments in leaf area were noticed in Pb-treated plants in comparison to the control plants (on average, 24.7%). In addition, root length was boosted in plants under Pb exposure (22.6–66.7%). In conclusion, *L. cultratus* is able to endure the exposure to high Pb concentrations in soil, being a potential plant species to be used for Pb phytostabilization in metal-contaminated soils in tropical regions.

Keywords *Cerrado* · Hormesis · Lead · Leguminous plants · Phytoremediation · Tolerance mechanism

Introduction

Agro-ecological disturbances have increased since the industrial revolution due to the intensification of anthropogenic activities (Wang et al. 2010; Carvalho et al. 2021). For instance, deforestation (Brasil 2015) and environmental contamination by natural and artificial compounds are already challenges for the current and next generations in some regions of the globe (Science Communication Unit 2013). Lead (Pb) is a naturally occurring trace element with no known function in organisms (Wang et al. 2010). Its concentration in superficial soil has been increased due to mining and smelting of Pb ores, coal burning, effluents from storage battery industries, and automobile exhausts (Verma and Dubey 2003). The problem is that Pb frequently triggers oxidation of cellular components and inactivation of enzymes and damages to DNA, posing a risk to living systems (Soares et al. 2019; Wang et al. 2010). The management of soils contaminated with heavy metals, which include Pb, is necessary to mitigate their impact on ecosystems, but the conventional physical and chemical methods employed for this purpose have the disadvantages of high cost, intensive labor, irreversible changes in soil properties, and/or disturbance of native soil microflora (Ali et al. 2013). In this context, the use of phytoremediation—a technology that employs plants to manage pollutants—is a cost-effective and eco-friendly alternative to recover heavy metal–contaminated environments (Lebrun et al. 2018).

However, most of the plants used for the phytoremediation of Pb-contaminated soils belong to the temperate climate. For

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instance, a high number of studies using the fast-growing woody species from genera *Populus* and *Salix* (poplar and willow, respectively) are easily observed in the literature (Ilić et al. 2020; Lebrun et al. 2018; Samuilov et al. 2016; Shi et al. 2019). By contrast, researches exploring the phytoremediation potential of native species from tropical regions are scarce, especially for woody plants (Souza et al. 2020). Therefore, we decided to search for candidate species in the Brazilian savanna (aka, Cerrado), which is the richest savanna in number of plant species in the world (Mendonça et al. 1998). *Cerrado* is the largest savanna region in South America, but the area of this biome was reduced by approximately 50% due to anthropogenic activities (Brasil 2015). Cerrado possesses challenging edaphoclimatic conditions (such as soil acidity, salinity, drought, and/or high levels of heavy metals), which generate selection pressures that may result in plant species with high tolerance to diverse abiotic stresses. Among the Cerrado's plant species, *Lonchocarpus cultratus* (Vell.) A.M.G. Azevedo and H.C. Lima is one of the most abundant species in several areas of South and Southeastern Brazil (Marcílio et al. 2019).

Evaluation of Pb content in *Cerrado's* soil is still incipient, but the available data suggest that the concentration of this non-essential trace element is generally below the threshold (i.e., 150 mg kg^{-1}) for agricultural purposes according Brazilian legislation (CETESB 2016; Ribeiro et al. 2019). For example, the lime generated from *Cerrado* region presented low Pb levels (on average, 30.5 mg kg^{-1} of soil) (Soares et al. 2015). Moreover, soil that was sampled in a transition region of the biomes *Cerrado-Mata Atlântica* had Pb concentrations that varied from 73.7 to 114.7 mg kg^{-1} (Longo et al. 2020). However, human activities are triggering Pb pollution in Cerrado, since elevated Pb concentration was observed in water, soil, bovine mineral supplements, plant- and animal-originated food, and human tissues (Gonçalves et al. 2009, 2010a, 2010b; Gomes et al. 2013; Miranda 2016; Mingoti et al. 2016; Nogueira et al. 2007). Such pollution was probably due to the use of Pb-contaminated mineral supplements to feed cattle and products necessary to grow crops (Gonçalves et al. 2000, 2009). Furthermore, *Cerrado* is facing serious environmental challenges by mining-related activities. For instance, two of the largest world mining disasters occurred in *Cerrado* region, both at *Minas Gerais* state, due to tailing dam collapse in 2015 and 2019 (Buch et al. 2020; Vergilio et al. 2020).

A key point is that *Cerrado* houses springs of several rivers of different relevant basins in the South America, including those from *Amazônica*, *da Prata*, e do *São Francisco* basins (Medeiros 2011), and problems related to the groundwater contamination, which is susceptible in *Cerrado*, demand the management of compounds that release heavy metals to the environment (Mingoti et al. 2016). Among the plant species from *Cerrado*, *Lonchocarpus cultratus* plays a fundamental role in the natural regeneration of devastated forest, due to its good adaptation to low-fertility soils in both dry and flooded areas (Marcílio et al. 2019; Panarari et al. 2004). Because of the high adaptability of *L. cultratus* to challenging environments, we hypothesize that this species may tolerate the exposure to Pb-contaminated soil. In this context, the present study aimed to evaluate the performance of *Lonchocarpus cultratus* grown in soil with increasing Pb levels (from 5, 56, 120, 180, and 292 mg kg^{-1}).

Materials and methods

Soil features and contamination

A Red Oxisol soil was used in the present experiment, and its physico-chemical features is in Table 1.

The Pb concentration chosen for this experiment was based in the range of soil Pb levels that are toxic to plants (from 100 to 500 mg kg^{-1}) according to Kabata-Pendias (2011). The artificial contamination of soil (which was performed before the sowing of seeds) was made by applying 400 mL of solutions containing different concentrations of lead acetate to the soil, which was manually homogenized (by using a concrete mixer and sieved in a 2 mm mesh) and incubated for 15 days. After the incubation period and just before the seed sowing, soil was sampled to analyze the Pb concentration that was available to plants. The Pb availability in soil was 5.2, 55.8, 120, 180, and 292 mg kg^{-1}.

Plant material and growing conditions

Seeds of *Lonchocarpus cultratus* (Vell.) Azevedo-Tozzi & H. C. Lima were supplied by the company "Sementes Caiçara." Only seeds with similar size and color were used in the present study. They were soaked in water for 4 h. Next, seeds were sown in 3 dm^3 plastic bags filled with 2 dm^3 of a Red Oxisol soil. Based in soil chemical analysis, nutrients were supplied to the plants (after 3 months of seed sowing) in order to avoid nutritional disorders; the amount of nutrient added to the soil was N (100 mg dm^{-3}); P (153 mg dm^{-3}); K (166 mg dm^{-3}); S (0.188 mg dm^{-3}); Zn (0.128 mg), and B (0.008 mg).

Leaf gas exchange

The evaluation of gas exchange in leaves of *L. cultratus* was performed by using a portable infrared gas analyzer (IRGA) (LI 6400xt, Li-Cor, Nebraska, USA) with photosynthetically active radiation of 1000 μmol m^{-2} s^{-1}. The photosynthetic (*A*, CO_2 μmol m^{-2} s^{-1}), stomatal conductance (*gs*, H_2O mol m^{-2} s^{-1}), and transpiration rates (*E*, mmol H_2O mol m^{-2} s^{-1}), as well as the internal CO_2 concentration (*Ci*, μmol CO_2 mol^{-1}), and ratio between internal and external CO_2 concentrations (*Ci/Ca*) were

Table 1 Soil chemical properties and texture

pH	O.M.	P	K	Ca	Mg	S	Al	V%	m%	CEC	B	Cu	Fe	Mn	Zn	Clay	Silt	Sand
4.3	48	37	144.3	320	144	35	36	31	11	103.7	0.33	3	49	49.4	3.4	48	13	38

Unit description of each soil parameter:
Unit: pH
$g.dm^{-3}$: O.M (organic matter)
mg dm^{-3} : P, K, Ca, Mg, S, Al, B, Cu, Fe, Mn, Zn
%: V% (base saturation), m% (aluminum saturation), clay, silt, and sand
Mmolc dm^{-3} : CEC (cation exchange capacity)

measured in newly, fully expanded leaves on the 170th day after seed sowing.

Leaf chlorophyll fluorescence

Chlorophyll a fluorescence was measured by using a fluorescence chamber attached to IRGA. The maximum fluorescence in dark-adapted leaves (*Fm*) and the maximum quantum yield of photosystem II (*Fv/Fm*) were evaluated between 20 and 22 h. The maximum fluorescence at steady-state (*Fv*) and light-adapted leaves (*Fm'*) were evaluated in between 7:30 am and 11h. The effective quantum yield of the PSII [Y (II)] and the quantum yield of non-photochemical quenching (NPQ) were estimated by using the following equations: Y (II) = (Fm′-Fv)/Fm′ and NPQ = (Fm-Fm′)/Fm′. All these evaluations were performed in newly, fully expanded leaves on the 170th day after seed sowing.

Plant biometry

Plants were harvested after 6 months of their cultivation (i.e., nearly on the 180 days after sowing), when the length (cm) of stems and the longest roots were measured with a ruler. The stem diameter (mm) was evaluated in the region immediately above the cotyledons scars using a digital caliper. For leaf area (cm^2) determination, detached leaves were measured by using a leaf area meter (LI-COR®, LI-3100). Moreover, samples of roots, stems, and leaves (which were divided in petioles and leaflets) were dried in a drying oven (60 °C) until a constant weight to determine their dry masses (Lima et al. 2019).

Lead extraction and quantification in soil and plant organs

The soil Pb extraction has been carried out in microwave-assisted acid digestion method (EPA 2007) and quantified in a Varian Vista MPX Inductively Coupled Plasma-Optical Emission Spectrometry (ICP-OES) with an axial torch, at 2020.353 ηm, whose detection limit is 0.05 μg mL^{-1}. To determine the Pb content in different plant tissues, they were dried at 65° C and then grounded. For each sample, 250 mg of the grounded tissues was digested in 2.5 mL of a 5:1 (nitric acid:perchloric acid), respectively, in a heat block at 120° C until cease the release of NO_2 (brown gas), and then the temperature was set to 200° C until cease the release of $HClO_4$ (white gas)—total time expended is between to 6 and 8 h. The resulting acid liquid containing Pb and other elements was cooled at room temperature and completed to 25 mL with deionized water, and it is called the acid extract which goes directly to the equipment. The quantification of Pb was carried out in a Perkin Elmer Atomic Absorption Spectrometer, model AAnalyst 200, whose detection limit is 0.02 μg mL^{-1}; using a Perkin Elmer 217 nm lamp, the analytical curve was made by using a standard Pb solution from Specsol® standards, and a blank read was performed previously to samples.

Lead content in plant, Pb translocation index, and percentage of Pb internalization

From the quantification of Pb concentration in plant organs and their respective biomass, the content of Pb in organs (Pb_O) was calculated through the formula:

$$\mathrm{Pb_O} = [Pb_O] x\ DW_O$$

where $[Pb_O]$ and DW_O are the Pb concentration in a given plant organ and the dry weight of this organ. The Pb translocation index (TI) was estimated by the following formula:

$$\mathrm{TI} = \frac{[Pb_{Sh}]}{[Pb_{Sh}] + [Pb_R]}$$

where $[Pb_{Sh}]$ and $[Pb_R]$ are the concentrations of Pb in shoots and roots, respectively.

Moreover, the percentage of Pb, which was added to the soil, that was internalized by the whole plant (IP) was estimated by the following formula:

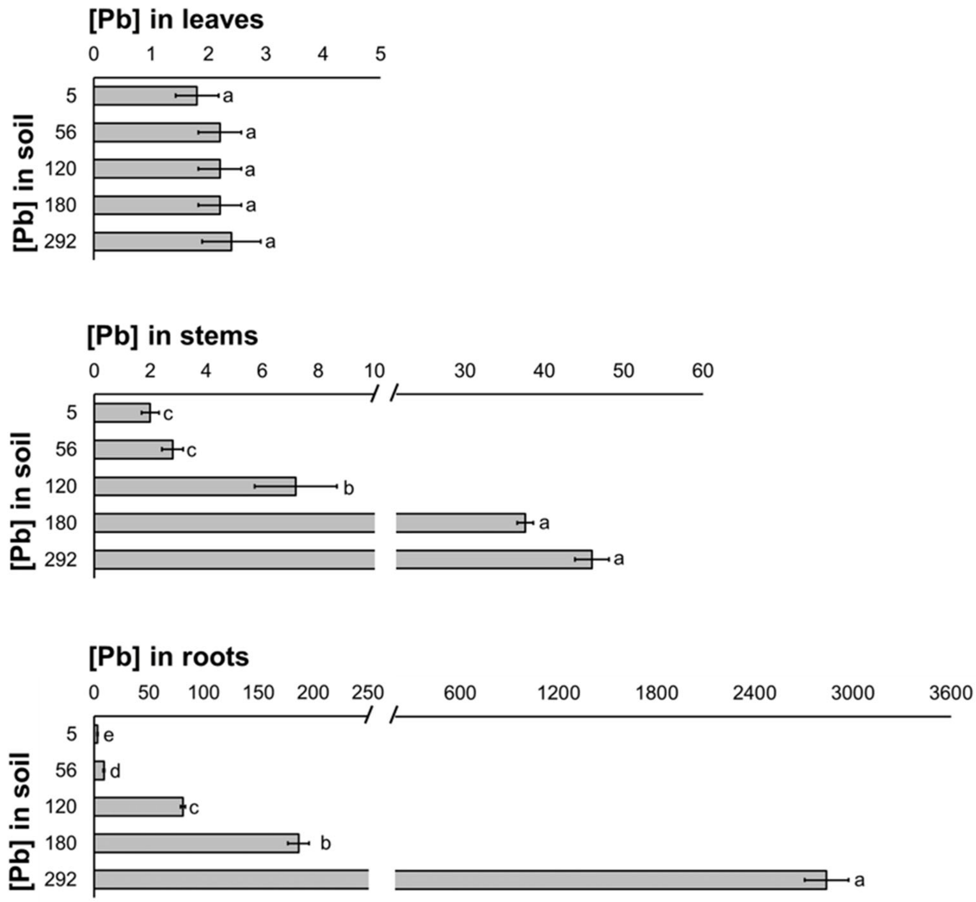

Fig. 1 Lead (Pb) concentration (μg g^{-1}) in leaves, stems, and roots of the leguminous tree species *Lonchocarpus cultratus* (Fabaceae) grown in soil containing increasing Pb concentrations (5, 56, 120, 180, and 292 mg kg^{-1}) for 6 months. Means followed by distinct letters differ by Duncan test ($p \leq 0.05$). $n = 5$.

$$\mathrm{IP} = \frac{Pb_p}{(Pb_S x\ 10)}$$

where Pb_P and Pb_S are the contents of Pb in the whole plant and soil, respectively.

Content of chlorophylls *a* and *b* in leaves

The content of chlorophylls *a* and *b* was indirectly estimated through a digital chlorophyll meter (clorofiLOG v.1.10, Falker Automação Agrícola Ltda) in the second newly and completely expanded leaves of the plants.

Statistical analysis

A completely randomized design was used in the experiment that contained five replications by treatment (i.e., Pb concentrations in soil), totalizing 25 experimental units. All variables were obtained from measurements in the five replications by treatment, except for Pb quantification in organs (for which three replications were used). Before analysis of variance (ANOVA), we evaluated whether the data were in accordance with the assumptions for ANOVA performance (i.e., normal distribution, variance homogeneity, and error independence) through the "Guided Data Analysis" tool of statistical software SAS (SAS Institute 2011). Data transformations and/or exclusions were performed when indicated by this tool. Data were subjected to one-way ANOVA ($p \leq 0.05$) through SAS® statistical software (SAS Institute 2011). If ANOVA presented significant *p*-values, data were subjected to Duncan test ($p \leq 0.05$) for comparison of means among treatments. After ANOVA, the transformed data were converted back to their original scale to plot figures, facilitating the comparison of treatments. Moreover, correlation analysis was performed through SAS® (i.e., "proc corr") (SAS Institute 2011) for some variables. In addition, principal component analysis (PCA) was performed in RStudio software (R Core Team 2019) FactoShiny package (Vaissie et al. 2020).

Results

Lead accumulation in plants

Increments in the soil Pb level from 5 (control soil) to 292 mg kg^{-1} provoked increases in Pb concentrations of roots (from 3 to 2840 mg kg^{-1}) and stems (from 2 to 46 mg kg^{-1}) of

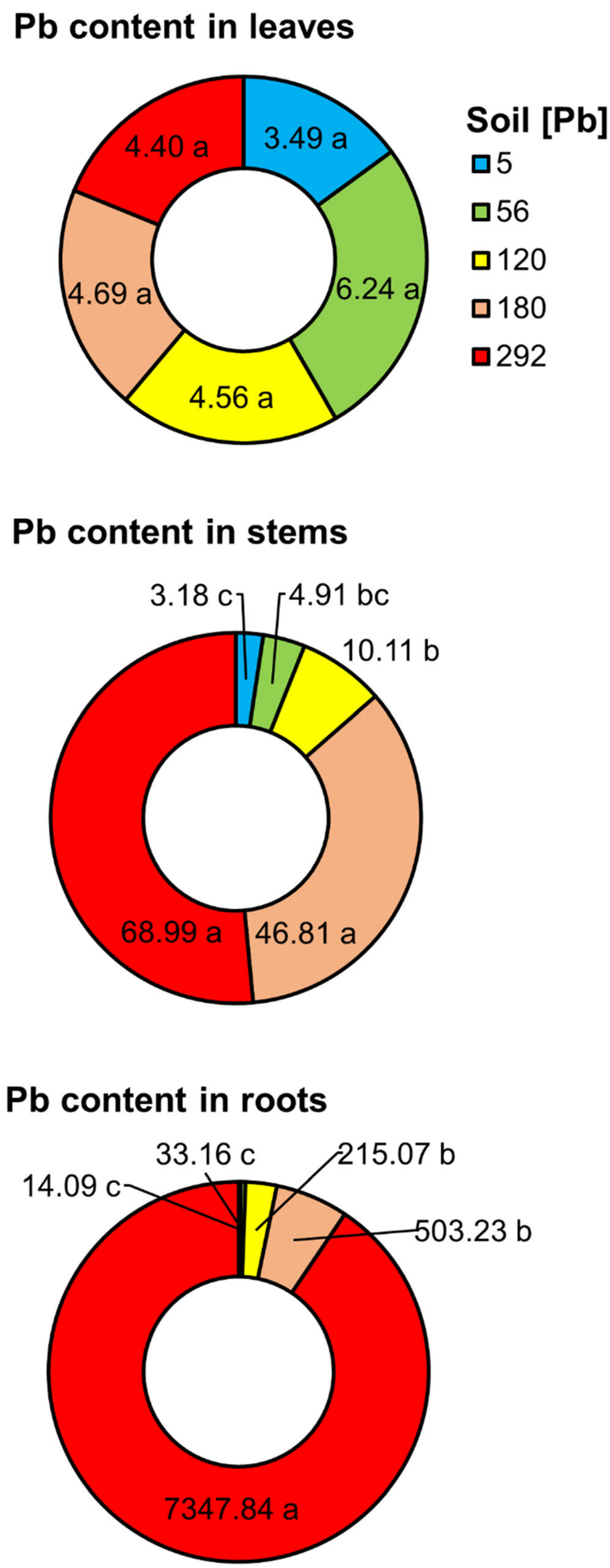

Fig. 2 Lead (Pb) content (μg organ^{-1} plant^{-1}) in leaves, stems, and roots of the leguminous tree species *Lonchocarpus cultratus* (Fabaceae) grown in soil containing increasing Pb concentrations (5, 56, 120, 180, and 292 mg kg^{-1}) for 6 months. Means followed by distinct letters differ by Duncan test ($p \leq 0.05$). $n = 5$.

L. cultratus (Fig. 1). However, Pb concentration in leaves was low and similar among Pb-treated and control plants, varying from 1.8 to 2.4 mg kg^{-1} (Fig. 1). Lead contents in different organs of *L. cultratus* had similar trends to those observed for Pb concentration: they were increased in stems and roots by increasing the Pb level in soil (Fig. 2). The Pb translocation index was highest in plants grown in soil with 5 and 56 mg kg^{-1} of Pb and decreased with the increasing Pb level in soil (Fig. 3). The percentage of Pb, which was added to the soil, that was internalized by the whole plant of *L. cultratus* was highest in plants grown in soil with the highest Pb at 292 mg kg^{-1} (Fig. S1).

Plant growth

Lead-treated plants presented an enhanced leaf area in comparison to the control plants (on average, 24.7%), reaching maximum values when they were grown in soil containing 56 mg kg^{-1} of Pb (Fig. 3). The root length was also incremented by exposure to Pb (up to 66.7%), especially in plants cultivated in soil with 56 and 292 mg kg^{-1} of this element (Fig. 3). The long-term exposure of *L. cultratus* to increasing Pb levels altered neither the biomass of roots, stems, and leaves (Table 2), nor the pattern of biomass partitioning among vegetative organs, stem length, root volume, and number of leaves (Table S1).

Leaf chlorophyll content, gas exchange, and photosynthetic performance

Transpiration and stomatal conductance were increased in plants subjected to 180 mg kg^{-1}, while *Ci/Ca* ratio was decreased in plants under exposure to 56 and 120 mg kg^{-1} in comparison to control plants (Fig. 3). The rate of CO_2 assimilation did not change by increasing Pb concentrations in soil (Table S2). The content of chlorophylls *a* and *b* was not affected by exposure of *L. cultratus* to increasing Pb concentration in soil (Table S2). Photosynthesis-related variables, such as *Fv/Fm*, were similar among treatments (Table S2).

Characterization of treatments by principal component analysis

The joined analysis of variables (which was significant by ANOVA at 5% plus those related to concentration and content of Pb in leaves) was able to segregate the plants grown

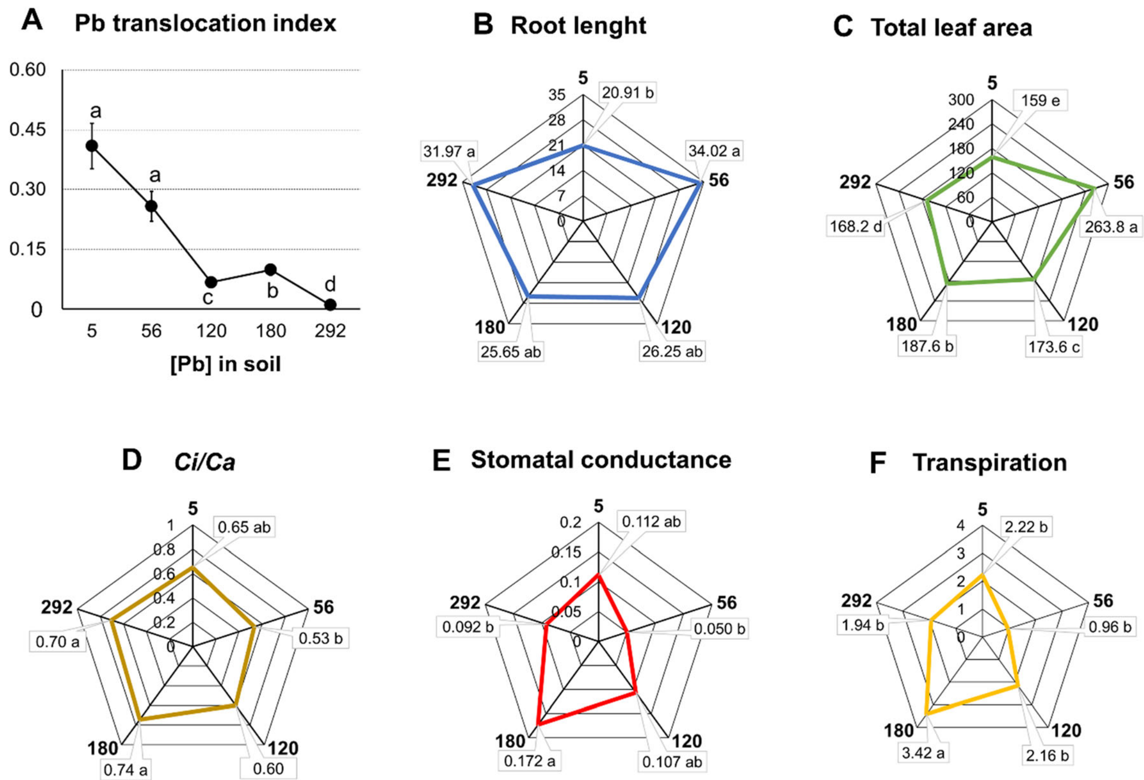

Fig. 3 Lead translocation index (**A**), root length (cm plant^{-1}, **B**), total leaf area (cm^2 plant^{-1}, **C**), ratio between internal and external CO_2 concentrations (*Ci/Ca*, **D**), stomatal conductance (mol H_2O m^{-2} s^{-1}, **E**), and transpiration (mol H_2O m^{-2} s^{-1}, **F**) in leaves of the leguminous tree species *Lonchocarpus cultratus* (Fabaceae) grown in soil containing increasing Pb concentrations (5, 56, 120, 180, and 292 mg kg^{-1}) for 6 months. Means followed by distinct letters differ by Duncan test ($p \leq 0.05$). $n = 5$.

in soil with Pb at 56, 180, and 292 mg kg^{-1} from each other and from the control plants (Fig. 4). Plants that were cultivated in the soil with 56 mg kg^{-1} were characterized by a well-developed leaf area and increased Pb content in leaves; plants that were grown in soil with 180 mg kg^{-1} were distinguished by the enhanced stomatal conductance and transpiration rates, and plants that were cultivated in soil with 292 mg kg^{-1} had an incremented Pb content in both roots and entire plants.

Discussion

The current study focused on the phytoremediation potential of a tree species from Brazilian savanna (aka, Cerrado), which is a poorly studied biome despite its great ecological relevance. Cerrado possesses challenging edaphoclimatic conditions (such as soil acidity, salinity, drought, and/or high levels of certain potentially toxic metals like Al), which generate selection pressures that may result in plant

Table 2. Root, stem, petiole, and leaf (RDM, SDM, PDM, and LDM, respectively) dry masses (g organ^{-1} plant^{-1}), root volume (RV, mL plant^{-1}), root length (RL, cm plant^{-1}), stem length (SL, cm plant^{-1}), and number of leaves (NL, unity plant^{-1}) of the leguminous tree species *Lonchocarpus cultratus* (Fabaceae) grown in soil with increasing lead (Pb) concentrations for 6 months.

[Pb]	RDM	SDM	PDM	LDM	RV	SL	NL
5	2.8 ± 0.7	1.3 ± 0.3	0.2 ± 0.1	1.6 ± 0.5	4.4 ± 1.1	11.4 ± 0.6	3.1 ± 0.5
56	3.4 ± 1.0	1.4 ± 0.3	0.3 ± 0.1	2.6 ± 0.7	7.3 ± 3.0	13.4 ± 1.5	4.9 ± 1.0
120	2.7 ± 0.3	1.2 ± 0.1	0.2 ± 0.0	2.0 ± 0.3	5.8 ± 1.4	12.0 ± 0.3	5.1 ± 0.4
180	2.8 ± 0.7	1.0 ± 0.2	0.2 ± 0.1	2.0 ± 0.7	7.0 ± 1.8	11.5 ± 1.0	5.6 ± 0.7
292	2.6 ± 0.7	1.1 ± 0.3	0.2 ± 0.1	1.9 ± 0.6	5.6 ± 0.9	12.8 ± 0.8	4.8 ± 0.5

ANOVA was not significant (p > 0.05) for these variables. $n = 5$.

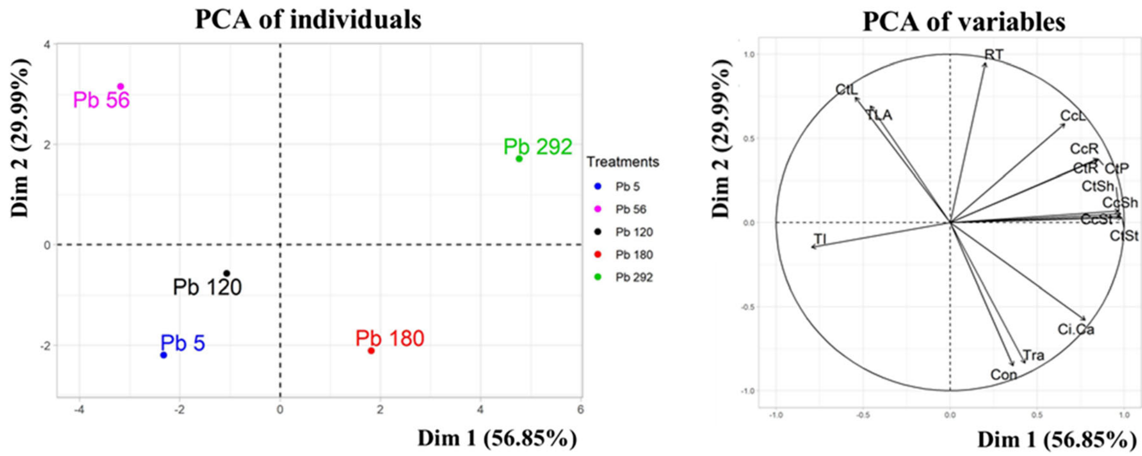

Fig. 4 Principal components analysis of diverse variables (which were related to the growth, gas exchange and plant capacity to accumulate and translocate lead—Pb) in the leguminous tree species *Lonchocarpus cultratus* (Fabaceae) grown in soil containing increasing Pb concentrations (5, 56, 120, 180, and 292 mg kg^{-1}) for 6 months. Total leaf area (TLA); root length (RT); stomatal conductance (Con); ratio between internal and external CO_2 concentrations (Ci/Ca); transpiration (Tra); lead (Pb) concentration in leaves, stems, shoots, roots, and in the entire plant (CcL, CcSt, CcR, CcSh, CcP, respectively); Pb content in leaves, stems, shoots, roots, and in the entire plant (CtL, CtSt, CtR, CtSh, CtP, respectively); and Pb translocation index (TI).

species with high tolerance to diverse abiotic stresses. Among the plant species in Cerrado, *L. cultratus* was chosen for the current study due to its good adaptation to low-fertility soils in both dry and flooded areas (Marcílio et al. 2019; Panarari et al. 2004).

Lonchocarpus cultratus endures long exposure to high Pb levels in soil

Lead toxicity is frequently noticed as decreased plant growth (Ilić et al. 2020; Mallhi et al. 2019; Muszyńska et al. 2020; Shi et al. 2019). However, the continuous development of *L. cultratus* in Pb-containing soil (Table 2, Fig. 3 and Supplementary Tables S1-2) shows that this plant species is able to acclimate to the long exposure to high Pb levels. Previous study also reported no Pb-induced impacts on the growth of *Vicia faba* plants (another fabaceous species) after their cultivation in soil containing Pb concentrations that ranged from 6.25 to 2000 mg kg^{-1} for 20 days (Wang et al. 2010). Moreover, Souza et al. (2012) have proven that the fabaceous species *Mimosa caesalpiniaefolia*, *Erythrina speciosa*, and *Schizolobium parahyba* were able to grow in soil contaminated with Pb concentrations higher than 500 mg dm^{-3}. From the practical point of view, our data indicates that *L. cultratus* is a strong candidate for phytoremediation of Pb-contaminated areas in tropics. Because most of Pb was accumulated in roots (Fig. 1), *L. cultratus* could be used for phytostabilization purposes. According to Ali et al. (2013), phytostabilization is one phytoremediation modality that aims to reduce the bioavailability of metals by stabilizing them in the rhizosphere or by accumulating them in roots. Taking into account that Cerrado harbors springs of several rivers of important basins in the South America (Medeiros 2011), the management of heavy metals by their stabilization in the root system of *L. cultratus* is a potential strategy that may help to mitigate possible contamination of the Brazilian savanna groundwater.

Reduced root-to-shoot Pb translocation avoids damages in photosynthetic organs

The low root-to-shoot Pb translocation (Fig. 3) reveals both the existence of protective mechanisms in roots for coping with high Pb accumulation and the occurrence of mechanisms to reduce Pb transference to the shoots. The higher production of heat shock proteins might be involved in the repair of damaged proteins or disposal of denatured proteins while avoiding cell apoptosis in roots of Pb-treated plants (Wang et al. 2010). Enhancements in the activity of antioxidant enzymes (such as superoxide dismutase and ascorbate peroxidase) and content of non-enzymatic antioxidants (such as glutathione, proline, anthocyanins, and flavonols) (Dias et al. 2019; Mallhi et al. 2019; Muszyńska et al. 2020) indicate the antioxidant system's role in the mitigation of Pb-induced oxidative stress. Plants were also able to modify their anatomy when challenged by Pb, altering the number and area of cortical parenchymal cells and percentage of vessels in roots (Ilić et al. 2020). Alterations in the anatomy of Pb-treated roots can be related (i) to the arrangement of cell wall components that may be involved in both Pb binding to the root cell walls (Chudzik et al. 2018), (ii) to the modifications in the root architecture, and (iii) to the avoidance of Pb translocation to shoots (Fig. 3). Changes in the root architecture, in turns, can be a plant attempt to improve water and nutrients and concurrently to get these resources in Pb-free patches of soil (Carvalho et al. 2020a).

Table 3. Pearson's correlation analysis among total leaf area (TLA); root length (RT); stomatal conductance (Con); ratio between internal and external CO_2 concentrations (Ci/Ca); transpiration (Tra); lead (Pb) concentration in leaves, stems, shoots, roots, and in the entire plant (CcL, CcSt, CcR, CcSh, CcP, respectively); Pb content in leaves, stems, shoots, roots, and in the entire plant (CtL, CtSt, CtR, CtSh, CtP, respectively); and root-to-shoot translocation index (TI) of lead (Pb) in the leguminous tree species *Lonchocarpus cultratus* (Fabaceae) grown in soil with increasing Pb concentrations for 6 months.

	TLA	RL	Con	Ci/Ca	Tra	CcL	CcSt	CcR	CcSh	CcT	CtL	CtSt	CtR	CtSh	CtT	TI
TLA	-	−45.29*	$-37.14\$$	−42.89*	−40.76*	5.84^{ns}	-26.02^{ns}	$-36.40\$$	−27.18	$-37.99^{\$}$	24.89^{ns}	-22.69^{ns}	-29.18^{ns}	-17.74^{ns}	-30.92^{ns}	$39.35^{\$}$
RL		-	-19.28^{ns}	2.53^{ns}	-27.15^{ns}	10.75^{ns}	20.38^{ns}	27.63^{ns}	26.09^{ns}	27.39^{ns}	6.43^{ns}	14.97^{ns}	25.14^{ns}	14.02^{ns}	16.62^{ns}	-26.93^{ns}
Con			-	58.99**	98.07***	32.00^{ns}	$37.57^{\$}$	16.34^{ns}	29.28^{ns}	17.33^{ns}	12.21^{ns}	22.21^{ns}	16.18^{ns}	21.13^{ns}	15.14^{ns}	-2.09^{ns}
Ci/Ca				-	53.56**	-10.43^{ns}	$36.95^{\$}$	40.93*	$38.01^{\$}$	41.39*	$-36.08\$$	11.61^{ns}	21.81^{ns}	5.48^{ns}	20.05^{ns}	$-34.19\$$
Tra					-	$34.91\$$	43.76*	18.61^{ns}	$34.75^{\$}$	19.84^{ns}	14.49^{ns}	28.73^{ns}	19.38^{ns}	27.06^{ns}	18.56^{ns}	-2.87^{ns}
CcL						-	15.85^{ns}	19.65^{ns}	22.60^{ns}	21.11^{ns}	71.31***	22.60^{ns}	29.49^{ns}	$34.16^{\$}$	27.03^{ns}	-21.32^{ns}
CcSt							-	90.42***	98.59***	90.97***	-1.394^{ns}	90.24***	87.15***	81.58***	82.22***	−69.13***
CcR								-	91.57***	99.72***	-1.77^{ns}	82.53***	95.95***	76.57***	94.69***	−91.49***
CcSh									-	92.59***	0.48^{ns}	88.36***	88.12***	81.92***	84.20***	−74.10***
CcT										-	-3.21^{ns}	82.23***	95.68***	76.27***	95.35***	−92.51***
CtL											-	25.48^{ns}	17.75^{ns}	43.34*	18.94^{ns}	5.43^{ns}
CtSt												-	91.05***	97.20***	86.89***	−63.78***
CtR													-	88.36***	96.52***	−87.44***
CtSh														-	87.96***	−60.53**
CtT															-	−94.66***
TI																-

***, **, *, and $^{\$}$ significant at 0.1, 1, 5, and 10%, respectively; *ns* non-significant

Photosynthetic apparatus plasticity and increased leaf area to sustain biomass production

The low Pb mobility to the aerial parts was previously associated with the mitigation of Pb-induced toxicity in aboveground parts of plants (Dias et al. 2019). Accordingly, the reduced chlorophyll content, which is a common outcome from metal toxicity (Muszyńska et al. 2020), was not detected in Pb-treated plants (Supplementary Table S2). When some Pb quantity reached shoots, this metal was preferentially accumulated in stems (r = 98.59%, p<0.0001, Table 3) of *L. cultratus*, revealing the existence of a secondary strategy to protect photosynthetic tissues by depositing Pb in stems rather than in leaves. Moreover, Pb-treated plants presented increments in the leaf area (up to 64.9%, Fig. 2) that means an increased potential to harvest light for photosynthesis, which may improve photosynthate production, allowing the maintenance of biomass production while sustaining plant strategies to overcome Pb-induced challenges (Carvalho et al. 2019; Carvalho et al. 2020b). Enhancements in both leaf area and root length reveal Pb-induced hormetic effects. Hormesis is the concentration-response phenomenon that is characterized by low-dose stimulation and high-dose inhibition, which is represented by U-shaped or inverted U-shaped dose-response curves depending on the variable under evaluation (Carvalho et al. 2020b). According to Agathokleous et al. (2020), hormesis allows plants to cope with environmental challenges within defined time windows, as an attempt to precondition plants to future larger environmental threats.

Conclusion

Overall, this study showed that *L. cultratus* is able to tolerate high Pb concentrations in soil by incrementing leaf area and root length, reducing Pb translocation to leaves and adjusting gas exchange behavior. From the practical point of view, data indicates that *L. cultratus* is a potential candidate to be used phytostabilization programs of Pb-contaminated soil in tropical regions. This information can help in the development of efficient management of Pb-polluted land aiming to decrease the impacts of trace elements on environment.

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