# 22 Physiology of Lead Accumulation and Tolerance in a Lead-Accumulating Plant (*Sesbania drummondii*)

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## CONTENTS



## ABSTRACT

A prerequisite for phytoremediation of heavy metal-contaminated sites is the identification of metal-accumulating plants. Although a few natural or induced metal accumulators tolerate and thrive under toxic concentrations of lead and other heavy metals, the specific mechanisms governing toxicity tolerance are not well understood. Plants respond to heavy metal toxicity in a variety of ways and have a range of potential mechanisms for the purpose of metal detoxification. *Sesbania drummondii*, a lead accumulator, displays evidence of cellular chelation of the metal with acetate and sulfur-rich compounds under x-ray absorption spectroscopic examinations. On the other hand, this plant uses antioxidative defense mechanisms effectively to counteract the oxidative stress that may be produced as a result of lead application. When grown in $Pb(NO_3)_2$ (500 mg/L), *Sesbania* had many folds enhanced activities of catalase and superoxide dismutase. Furthermore, photosynthetic efficiency ($F_v/F_m$) and integrity ($F_v/F_0$) of this plant were largely maintained at this concentration of lead.

## 22.1 INTRODUCTION

Lead (Pb) contamination in soil is a widespread phenomenon and originates from automobiles, metal-smelting plants, mines, lead-contaminated sewage sludge, industrial wastes, etc.[1]. Lead concentration in roadside fields is sharply elevated due to heavy traffic, particularly in industrialized areas [2,3]. Severe Pb contamination of soil is associated with a variety of environmental problems, including loss of vegetation, ground water contamination, and Pb toxicity to plants, animals, and humans [4]. Thus, there is an urgent need for remediation of contaminated sites using an effective and environmentally friendly technology such as phytoremediation.

Heavy metal accumulation by plants has been utilized in various phytoremediation strategies for decontamination of the environment [5–8]. One of the key goals in phytoextraction is to select plants (hyperaccumulators) that can translocate substantial amounts of toxic metals from their roots to aerial parts, which can be easily harvested. For a plant species to be efficient in lead phytoextraction, it should accumulate metal concentration > 0.1% of shoot dry weight, in addition to having high biomass productivity. A critical balance between metal accumulation and plant biomass productivity will make a plant more efficient for phytoextraction [5]. From this standpoint, plant species such as Indian mustard, pea, and corn were the focus of recent Pb phytoremediation research. These species accumulate high amounts of lead and generate satisfactory biomass [6–8].

Another interesting Pb accumulator is *Sesbania drummondii*, a large, bushy perennial plant with high biomass productivity that grows naturally in seasonally wet places of the southern coastal plains of the U.S. It demonstrates a unique potential of Pb accumulation in aerial parts from an aqueous solution [9]. When grown in Pb-contaminated soil in a greenhouse, this species showed a substantial movement of Pb from roots to shoot with appreciable amounts accumulated in the aerial parts [10]. If its accumulation potential is considered with respect to the enormous biomass (10 to 15 ton/ha/year) that this plant can generate, *Sesbania* should qualify as one of the best known Pb accumulators. Though *Sesbania* and other plant species tolerate and accumulate toxic concentrations of Pb, the specific mechanisms are not well understood. Therefore, understanding the physiological and biochemical basis of metal accumulation will be helpful in chalking out phytoremediation strategy.

Plants have a range of potential mechanisms at the cellular level that might be involved in detoxification and thus tolerance to heavy metal stress. Chelation of metals in the cytosol by high-affinity ligands is potentially a very important mechanism of heavy metal detoxification and tolerance [11]. A number of ligands have now been recognized and their roles have been reviewed. In general, they include amino acids, organic acids, and peptides such as the phytochelatins and the metallothioneins [12]. The phytochelatins (PCs) have been most widely studied in plants, particularly in relation to Cd and Zn [13]. PCs are a family of metal-complexing peptides that have a general structure (y-Glu-Cys)*n*-Gly, where $n$ = 2 to 11, and are rapidly induced in plants in response to exposure to heavy metals [14,15]. Few reports, however, have appeared demonstrating the production of PC in response to Pb toxicity in plants, particularly those belonging to higher plants [16]. Biochemical evidence indicates that plants exposed to toxic metals may produce ligands for metal detoxification or transport, or both [17]. The internal speciation of Pb in *Sesbania* tissues was examined using x-ray absorption near-edge structure (XANES) and extended x-ray absorption fine structure (EXAFS) [18].

Earlier studies suggest that exposure to Pb and other heavy metals generally interferes with photosynthetic activity, severely affecting health of plants [19–21]. A variety of mechanisms work in tandem to counteract the effects of oxidative stress produced as a result of heavy metal (Pb) accumulation in plant cells [22–24]. Oxidative stress and effects of reactive oxygen species are generally handled by a number of antioxidant enzymes, such as superoxide dismutases, peroxidases, and catalases. Superoxide dismutase (SOD), the first enzyme in the detoxifying process, converts superoxide anion — a powerful reactive oxygen species — to hydrogen peroxide [25]. Hydrogen peroxide ($H_2O_2$) is scavenged directly by catalase (CAT), which converts it to water and molecular oxygen. Peroxidases also scavenge $H_2O_2$ indirectly by combining it with antioxidant compounds such as ascorbate and guaiacol [23,24,26]. Measurement of activities of antioxidative enzymes can thus be used to indicate oxidative stress in plants [22]. Thus, accumulation of high amounts of metals in the hyperaccumulator plant suggests the existence of a strong antioxidative defense mechanism to avoid the harmful effects.

This chapter describes

- Uptake and transport of Pb in Pb-accumulating plants
- X-ray absorption spectroscopic analysis to demonstrate biotransformation of accumulated Pb in *Sesbania* tissues
- Use of effective antioxidative defense mechanisms
- Effect of Pb accumulation on photosynthetic activities in *Sesbania* species

## 22.2 LEAD ACQUISITION AND TRANSPORT

### 22.2.1 Factors Governing Lead Uptake by Plants

Accumulation of Pb by plants depends on several factors, the most important of which are the genetic capability of the plant, as in a hyperaccumulator, and Pb bioavailability. The limiting factor for metal accumulation is the amount of Pb readily available for uptake. The solubility of Pb in soil is limited due to complexation with organic matter, sorption on clays and oxides, and precipitation as carbonates, hydroxides, and phosphates [27]. The application of a synthetic chelator has been used to increase Pb solubility in soil solution and EDTA has been found to be a most effective chelating agent for Pb desorption [7,8,28].

The chemistry and physiology of EDTA–Pb complex is understood better than that of any other Pb–chelate complex. When EDTA is added to Pb-contaminated soil, it complexes with soluble Pb. Due to high affinity of EDTA for Pb, the Pb–EDTA complex formation dominates other metal–EDTA complexation in most soils between pH 5.2 and 7.7 [29]. The soluble soil Pb concentration is not the only factor that influences its uptake in plants. Epstein et al. [30] observed substantially higher Pb accumulations in plants grown in soil containing 4.8 mmol Pb/kg soil and amended with 1 mmol EDTA/kg soil than in plants grown in soil containing 1.5 mmol Pb and 5 mmol EDTA/kg soil. This indicates that a higher ratio of Pb:EDTA in the soil solution will result in enhanced Pb uptake by the plant.

Thus, only a careful consideration of chelate application, taking into account factors like soil type and its total Pb content, can enhance the efficacy of a phytoextraction strategy. EDTA has been shown not only to enhance Pb desorption from the soil components to the soil solution but also to increase its transport into the xylem and its translocation from roots to shoots [7,30–32]. Vassil et al. [32] demonstrated that Pb accumulation in shoots is correlated with the formation of Pb–EDTA in the hydroponic solution and that Pb–EDTA is the major form of Pb taken up and translocated by the plant via xylem stream. The physiological basis of the uptake of Pb–EDTA and, particularly, the possibility of this large molecule to cross the cell membrane are unknown. However, using extended x-ray absorption fine structure spectroscopy, Sarret et al. [16] confirmed the presence of a substantial amount of Pb–EDTA in *Phaseolus vulgaris* leaves, when this plant was grown in a solution of Pb–EDTA.

### 22.2.2 Mode of Lead Transport

Electron microscopic techniques have mapped out Pb transport via various plant tissues [31,33–35]. Patterns of Pb migration and deposition in tissues differ depending on whether the supply of Pb is in chelated or unchelated form. In *Pinus radiata*, it has been shown in ultrathin sections that Pb grains were exclusively distributed in the outermost layer of the root cell wall and in negligible amounts in the needle when Pb was supplied in unchelated form. Conversely, when Pb was supplied in chelated (EDTA or HEDTA) form, higher intensities of Pb fine grains were detected in needle and the least in the root sections [31]. These ultramicroscopic observations are in conformity with the earlier uptake results in Indian mustard [6], where most lead was accumulated in roots on supply of Pb in the unchelated form.

In *P. radiata* roots, Pb supplied in unchelated form was not found in vacuoles, dictyosomes, or intercellular spaces, but it was often found embedded in or adjacent to cell wall — in many cases, near plasmodesmata [31]. This situation in *P. radiata* suggests that, in the case of Pb deposition between the cell wall and the cell membrane, it is probable that it was transported apoplastically. However, in the case of its aggregation within plasmodesmata, the mode of transport might have been symplastic. Occurrence of two simultaneous modes of Pb transport has also been advocated in other cases [33,36]. Transmission electron microscopic examination coupled with x-ray microanalysis of *Sesbania* root showed Pb deposits along the plasma membrane of the cells. The smaller granules appeared to coat the surface of the plasma membrane while larger deposits, looking like globules, extended deeper into the cell wall [9]. A large deposit was observed in high magnification within the tonoplast of the vacuole [9,18]. This is an indication of symplastic mode of transport in *Sesbania*, though not excluding the possibility of apoplastic migration.

This brings up the question of how *Sesbania* cells capture Pb particles. The fact that it was not detected in the ground cytoplasm but only in the plasma membrane and vacuole may suggest that endocytosis also plays a role in Pb uptake in this species. Reports of pinocytosis or endocytosis as a device for Pb entrapment are also available in the literature [31,35].

Whether following apoplastic or symplastic routes, Pb must cross the Casparian strip-barrier of the root in order to reach the xylem stream; this is difficult for the large Pb particles due to their size and charge characteristics. However, once they have formed a complex with a chelator such as EDTA, their solubility increases and thus the particle size may also decrease. As a result, the complex may become partially invisible to those processes that would normally prevent unrestricted movement, such as precipitation with phosphates or carbonates or binding to cell walls through mechanisms such as cation exchange.

Thus, the general agreement is that synthetic chelates overcome barriers to translocation. Now, how does Pb enter the vessels or tracheids of the xylem having moved symplastically to the parenchyma cells of the vascular cylinder? The mechanism by which transfer of Pb particles from vascular cylinder parenchyma to vessels or tracheids occurs may be a type of highly selective active-carrier transport, as opposed to facilitated diffusion [37]. Translocation of Pb from root to shoot via xylem has been shown in many studies [6,38,39].

## 22.3 SPECIATION OF ACCUMULATED LEAD IN A LEAD ACCUMULATOR

### 22.3.1 CHARACTERISTICS OF XANES IN *SESBANIA* SAMPLES

Currently, speciation of Pb in plant tissues (roots and leaves) has been studied by Sharma et al. [18] using $L_{III}$-edge XANES spectra (Figure 22.1A and B). The fittings of the XANES based on linear combination analysis are depicted in Table 22.1. The root sample grown in presence of Pb primarily consisted of a lead (II) acetate type of structure; over 60% of the spectra was defined by the lead (II) acetate structure (Table 22.1). The remaining part of the lead bound to the roots comprised mainly lead (II) nitrate, lead (II) sulfide, and lead metal (10, 20, and 9%, respectively).

This indicates that *Sesbania* physiologically transforms the starting material, lead (II) nitrate, into organic type lead compound, Pb acetate. The plant leaf sample demonstrated even more changed composition consisting predominantly of lead acetate (52%), lead sulfate (26%), and lead sulfide (14%). The low percentage of the lead nitrate (7.6 %) found in the linear combination

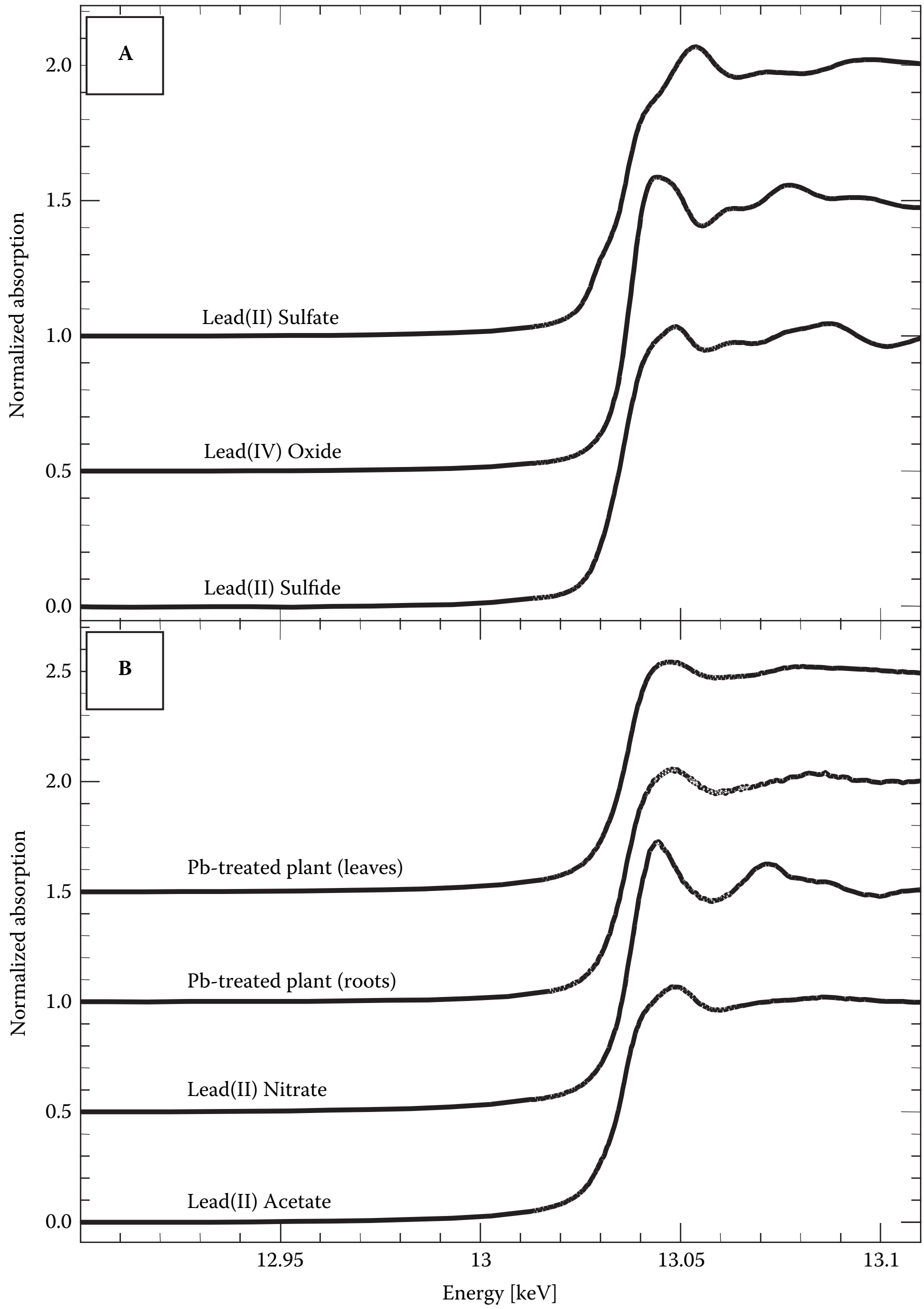


**FIGURE 22.1** (A) X-ray absorption near edge structure of lead model compounds: lead (II) sulfide, lead (II) sulfate, and lead (IV) oxide. (B) X-ray absorption near edge structure of lead-treated *Sesbania drummondii* samples, lead (II) nitrate, and lead (II) acetate. (From Sharma, N.C. et al., *Environ. Toxicol. Chem.*, 23, 134, 2004. With permission.)

XANES fitting data is another evidence in favor of biological transformation of lead (II) nitrate into organic types of structures, possibly for storage of the lead into or onto cellular material. It is interesting to note that speciation of Pb into lead acetate does not occur in the starting solution [16].

**TABLE 22.1**
**LC-XANES Fittings of *Sesbania drummondii* Exposed to 500 mg/L $Pb(NO_3)_2$ Using Lead (II) and (IV) Model Compounds**

| Samples | % $PbNO_3$ | % $PbSO_4$ | % Pbmetal | % PbS | % Pb acetate |
|---|---|---|---|---|---|
| Leaves | 7.6 | 25.8 | 0.0 | 14.2 | 52.4 |
| Root | 10.1 | 0.0 | 8.8 | 20.2 | 60.9 |

*Source:* Sharma, N.C. et al., *Environ. Toxicol. Chem.*, 23, 134, 2004. With permission.

### 22.3.2 Characteristics of EXAFS in *Sesbania* Samples

EXAFS features (Figure 22.2A and B) and FEFF fittings (Table 22.2 and Table 22.3) shown by Sharma et al. [18] indicate that lead in the root and leaf samples is bound into a chemical moiety with interatomic distances similar to lead (II) acetate. Though the root sample of *Sesbania* displays spectra comparable to the lead (II) acetate type of structure, the presence of a secondary complex complicates the interpretation. The FEFF fittings of root sample, however, indicate a ten-coordinate system that has a mixture of different compounds including lead particles. At the same time, the leaf sample shows an octahedral coordination, making EXAFS interpretation easy. XANES fittings of leaf sample are simple in composition, showing absence of lead particles. Though both samples are complex, they contain compounds of similar structure and composition, as indicated by XANES structure.

Presence of lead acetate in large proportions (>50%) in both the samples (Table 22.1) suggests transport of lead via Pb–organic acid complex. Metal–organic acid complexation has been reported as a phase of metal transport in a variety of plants [17,40,41]. In *Phaseolus vulgaris*, formation of various lead complexes including Pb–salicylate was reported when plants were grown in medium containing Pb and EDTA. Cerussite (lead carbonate) was found to be the predominant Pb species in leaves when *Phaseolus* plants were grown in solution containing $Pb(NO_3)_2$ alone.

The evidence for sulfur ligands is a potentially unique aspect of lead speciation in *Sesbania* species. Though sulfur is present in both the samples, the proportion in leaf is double the root content. The nature of sulfur complex also varies. Leaves contain $PbSO_4$ and PbS, but roots have only PbS. These ligand properties are indicative of glutathione (γ-Glu-Cys-Gly) and phytochelatins, small metal-binding polypeptides with the amino acids sequence (γ-Glu-Cys)*n*- Gly, where $n = 2$ to 14. Phytochelatins ($PC_s$) play an important role in heavy metal homeostasis and detoxification [42] and their induction has been reported as an effective strategy against Cd toxicity [12,43]. A recent study suggested that $PC_s$ might also be involved in arsenic detoxification [44]. Reports of PC induction in response to Pb toxicity are not common in higher plants [16]. However, Pb-induced PC synthesis was confirmed in a common microalga, *Stichococcus bacillaris* [45].

## 22.4 ANTIOXIDATIVE DEFENSE IN A LEAD ACCUMULATOR

### 22.4.1 Catalase Activity in *Sesbania* Seedlings

Catalase activities of *Sesbania drummondii* seedlings grown in the absence or presence of 500 mg/L $Pb(NO_3)_2$ were determined by Ruley [10]. The enzyme activities in Pb-treated seedlings increased dramatically, >300% higher than the respective values of controls at week 4 (Figure 22.3). In *Thlaspi caerulescens*, a constitutive Cd hyperaccumulator, an elevated catalase induction in response to Cd stress has been demonstrated [46]. An accumulator of Pb, *Pisum sativum* [7], also demonstrated an elevated activity of CAT in response to 104 or 207 mg/L Pb [47].

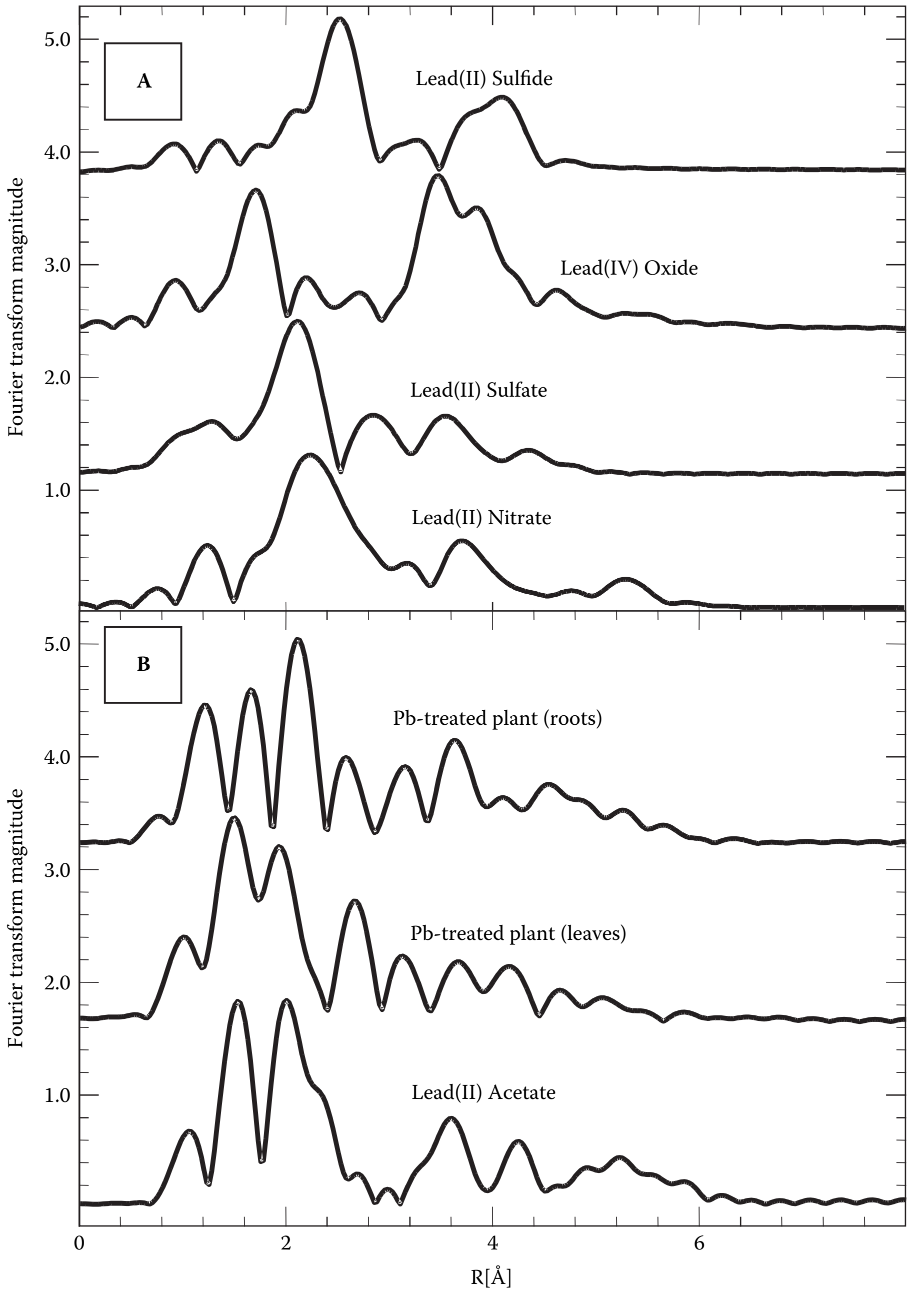


**FIGURE 22.2** (A) Extended X-ray absorption fine structure of lead model compounds: lead (II) nitrate, lead (II) sulfide, lead (II) sulfate, and lead (IV) oxide. (B) Extended X-ray absorption fine structure of lead-treated *Sesbania drummondii* samples and lead (II) acetate. (From Sharma, N.C. et al., *Environ. Toxicol. Chem.*, 23, 134, 2004. With permission.)

## 22.4.2 SOD Activity in *Sesbania* Seedlings

Superoxide dismutase (SOD) activities in the absence and presence of 500 mg/L $Pb(NO_3)_2$ were also reported by Ruley [10]. SOD activities in Pb-treated seedlings gradually increased and were recorded to be >200% higher than the respective values of controls at week 4 (Figure 22.4). Similar

**TABLE 22.2**
**Compilation of Structural Parameters Extracted from Extended X-Ray Absorption Fine Structure Spectra of *Sesbania drummondii* Exposed to 500 mg/L $Pb(NO_3)_2$**

| Neighboring atom | Coordination number | R Å[a] | $S^{2(b)}$ |
|---|---|---|---|
| **Leaves** | | | |
| Pb-O | 2.0 | 1.90 | 0.0039 |
| Pb-C | 2.0 | 2.20 | 0.00086 |
| Pb-S | 2.0 | 2.85 | 0.0059 |
| **Roots** | | | |
| Pb-O | 1.2 | 1.80 | 0.000051 |
| Pb-C | 1.0 | 2.01 | 0.0017 |
| Pb-O | 1.2 | 1.99 | 0.0016 |
| Pb-O | 1.9 | 2.78 | 0.0099 |
| Pb-O | 1.6 | 2.75 | 0.0070 |
| Pb-O | 1.6 | 2.57 | 0.0099 |

Distance in angstroms from the metal to the neighboring atom.
[b]Squared standard deviation.

*Source:* Sharma, N.C. et al., *Environ. Toxicol. Chem.*, 23, 134, 2004. With permission.

to catalase activity, a significant increase in the activity of SOD has been reported in *Pisum sativum* [47]. A hyperaccumulator of Cd, *Alyssum argenteum*, has also been reported to exhibit an elevated SOD activity in response to high concentrations of Cd [48].

### 22.4.3 GPX Activity in *Sesbania* Seedlings

The guaiacol peroxidase (GPX) activities of *Sesbania drummondii* seedlings grown in 500 mg/L $Pb(NO_3)_2$ have also been determined [10]. Controls experienced a significant, but temporary, increase in GPX activity at week 2, returning to their original level by week 4 ($p > 0.05$) (Figure 22.5). GPX activities of plants exposed to Pb showed a steady increase during the growth period, registering a level significantly higher than that in control ($p < 0.05$) (Figure 22.5). Increased activities of peroxidase in response to Pb exposure in *Sesbania* are comparable to those reported in a Pb-tolerant species, *Sonchus oleraceus*, in which similar increases in activities of peroxidase were observed [24]. *Phaseolus vulgaris* also demonstrated increased activities of GPX and APX (ascorbate peroxidase) on exposure to 115.8 mg/L Pb–EDTA [22].

## 22.5 PHOTOSYNTHETIC ACTIVITY IN A LEAD ACCUMULATOR

### 22.5.1 Efficiency of Photosynthetic Apparatus in *Sesbania*

Seedlings grown in liquid medium contaminated with 500 mg/L Pb $(NO_3)_2$ were assessed for photosynthetic activity by measuring chlorophyll *a* fluorescence parameters using the Handy-PEA instrument (Hansatech Instruments, U.K.) [10,20]. The following fluorescent parameters were measured: $F_o$ ( minimum chlorophyll *a* fluorescence after the dark adaptation) and $F_m$ (maximum fluorescence after the pulse of red light). From these two measurements, the $F_v$ (variable fluores-

**TABLE 22.3**
**Compilation of Structural Parameters Extracted from Extended X-Ray Absorption Spectra of Model Compounds**

| Neighboring atom | Coordination number | R Å[a] | S2(b) |
|---|---|---|---|
| **$PbO_2$** | | | |
| Pb–O | 2.28 | 2.19 | 0.00035 |
| Pb–O | 3.7 | 2.33 | 0.0039 |
| Pb–Pb | 2.0 | 3.36 | 0.0015 |
| **$PbSO_4$** | | | |
| Pb–O | 1.0 | 2.65 | 0.0051 |
| Pb–O | 1.0 | 2.57 | 0.00084 |
| Pb–O | 2.0 | 2.73 | 0.0010 |
| Pb–O | 2.0 | 2.86 | 0.0021 |
| Pb–O | 2.0 | 2.98 | 0.0048 |
| Pb–O | 2.0 | 3.14 | 0.0044 |
| Pb–O | 2.0 | 3.33 | 0.0011 |
| **PbS** | | | |
| Pb–S | 6.12 | 2.98 | 0.0065 |
| Pb–Pb | 11.3 | 4.22 | 0.0080 |
| **$Pb(NO_3)_2$** | | | |
| Pb–O | 6.73 | 2.73 | 0.0064 |
| Pb–O | 5.36 | 2.87 | 0.0057 |
| Pb–N | 4.89 | 3.24 | 0.0039 |
| **Pb acetate** | | | |
| Pb–O | 1.0 | 1.88 | 0.0025 |
| Pb–C | 1.0 | 2.10 | 0.0071 |
| Pb–O | 1.0 | 1.89 | 0.0036 |
| Pb–O | 3.0 | 2.47 | 0.0046 |
| Pb–O | 1.0 | 3.01 | 0.0067 |
| Pb–C | 1.0 | 2.82 | 0.0019 |
| Pb–O | 1.0 | 3.20 | 0.0058 |
| Pb–C | 1.0 | 1.74 | 0.0049 |

[a] Distance in angstroms from the metal to the neighboring atom.
[b] Squared standard deviation.

*Source:* Sharma, N.C. et al., *Environ. Toxicol. Chem.*, 23, 134, 2004. With permission.

cence calculated as the difference between the minimal and maximal fluorescence), $F_v/F_m$ (ratio of variable to maximal fluorescence), and $F_v$ $F_o$ (ratio of variable to minimal fluorescence) were determined.

$F_v/F_m$ value is an indicator of the metabolic status of plants [49]. An $F_v/F_m$ ratio of 0.8 or above is characteristic of a healthy plant [19]. *Sesbania* seedlings grown in the presence and absence of Pb had $F_v/F_m$ values of 0.8 or higher, except at week 4, when the experimental plants showed lower value (0.78) significantly different from that of the control (Figure 22.6).

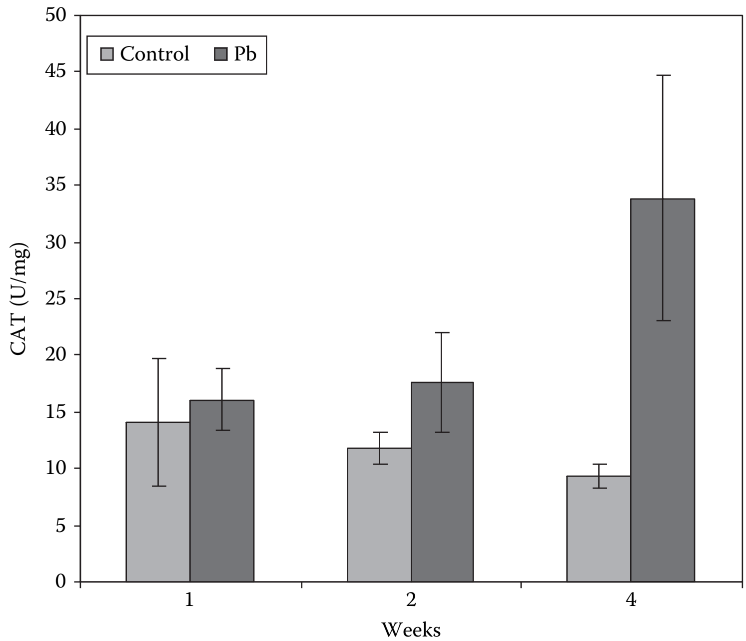


**FIGURE 22.3** Catalase activities (U mg$^{-1}$ FW) of *Sesbania drummondii* seedlings grown in the presence of 500 mg/L $Pb(NO_3)_2$ for 4 weeks. Values represent means and SE ($n$ = 6).

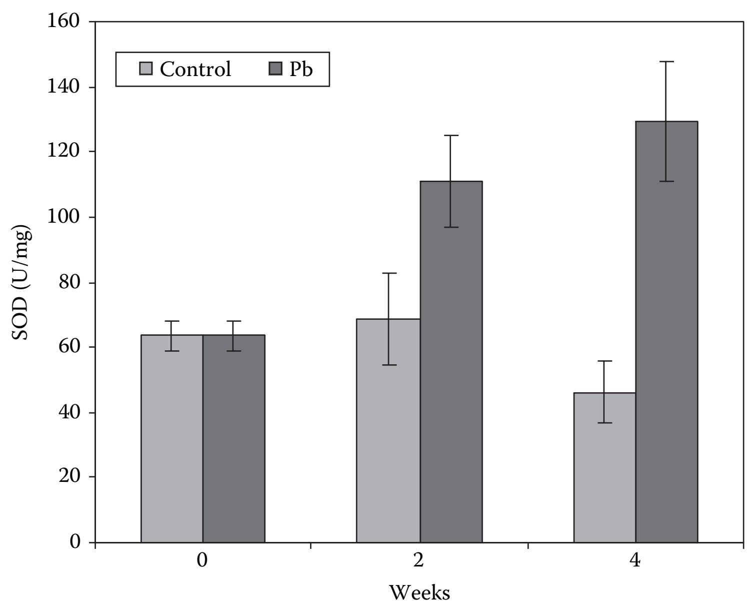


**FIGURE 22.4** Superoxide dismutase activities (U mg$^{-1}$ FW) of *Sesbania drummondii* seedlings grown in the presence of 500 mg/L $Pb(NO_3)_2$ for 4 weeks. Values represent means and SE ($n$ = 6).

### 22.5.2 Active Photosynthetic Reaction Centers in *Sesbania*

$F_v/F_o$ (ratio of variable to minimal fluorescence) indicates the size and number of active photosynthetic centers in the chloroplast and therefore the photosynthetic strength of the plant. $F_v/F_o$ value of 4.0 or more indicates that the plant is healthy and not suffering photosynthetic stress [19].

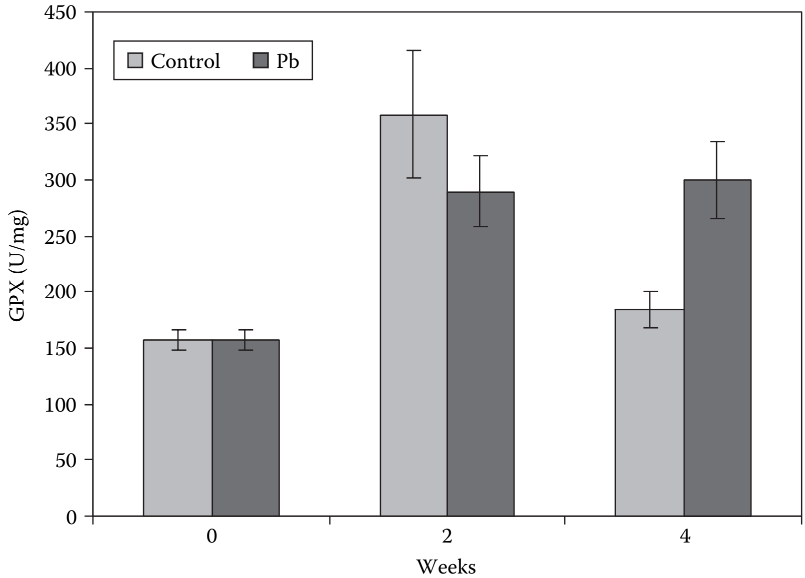


**FIGURE 22.5** Guaiacol peroxidase activities (U mg$^{-1}$ FW) of *Sesbania drummondii* seedlings grown in the presence of 500 mg/L $Pb(NO_3)_2$ for 4 weeks. Values represent means and SE ($n$ = 6).

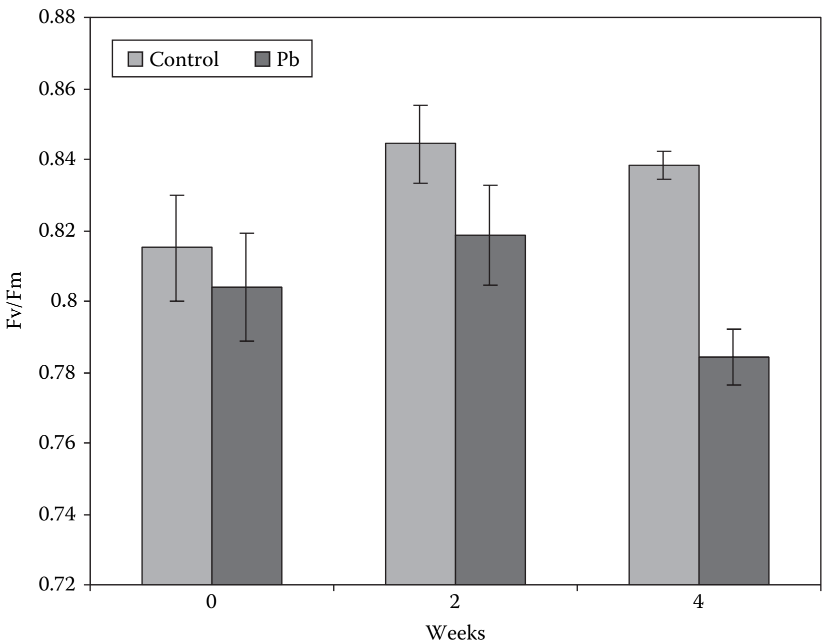


**FIGURE 22.6** $F_v/F_m$ values of *Sesbania drummondii* seedlings grown in the presence of 500 mg/L $Pb(NO_3)_2$ for 4 weeks. Values represent means and SE ($n$ = 6).

*Sesbania* seedlings grown in the presence and absence of 500 mg/L Pb (as described earlier), displayed $F_v/F_o$ values equal to 4.0 or higher up to week 2. However, in week 4, values dropped off to 3.7 for the experimental group (Figure 22.7) without discernable symptoms.

Though Pb or other heavy metals have been reported to affect photosynthetic activity in plants, *S. drummondii* had little or no effect on photosynthetic activity on exposure to Pb. The photosyn-

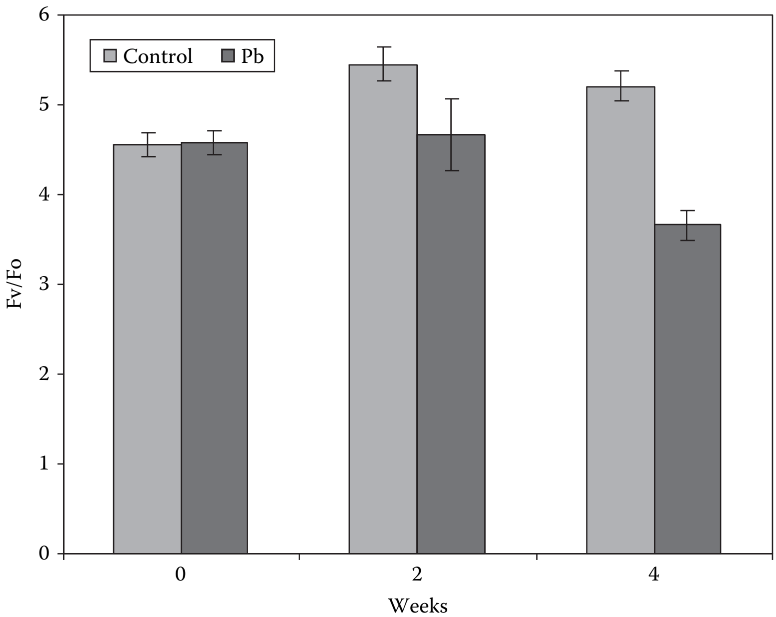


**FIGURE 22.7** $F_v/F_o$ values of *Sesbania drummondii* seedlings grown in the presence 500 mg/L $Pb(NO_3)_2$ for 4 weeks. Values represent means and SE ($n = 6$).

thetic efficiency of *Sesbania* was more or less comparable to *Pelargonium* sp., where $F_v/F_m$ and $F_v/F_o$ were not significantly affected by Pb accumulation [20]. It is known that Pb interferes directly with δ-aminolevulinic acid dehydratase, an important enzyme in the formation of chlorophyll in plants [16]. This affects chlorophyll synthesis and carbon assimilation, eventually modifying the photolysis of water. The altered $H_2O$ photolysis generates reactive oxygen species (ROS) such as superoxide ($O_2^-$) and hydroxyl radicals (·OH) [22–24].

## 22.6 CONCLUSION

Understanding the physiology of metal accumulation and detoxification mechanisms in plants is crucial to developing strategy for heavy metal remediation. Evidence suggests that *Sesbania drummondii* uses more than one mechanism to counteract lead toxicity. $Pb^{2+}$ in *Sesbania* tissues complexes predominantly with acetate- and sulphur-containing compounds to minimize the toxic effects; however, antioxidative defense mechanisms are also used by this plant effectively to overcome the effects of reactive oxygen species and protect the photosynthetic machinery and efficiency. On the basis of biomass generation capability and physiological backup for tolerance, this plant can be a suitable agent for remediation of lead-contaminated sites.

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