

Review

Metal uptake, transport and release by wetland plants: implications for phytoremediation and restoration

Judith S. Weis^{a,*}, Peddrick Weis^b

^aDepartment of Biological Sciences, Rutgers University, Newark, NJ 07102, USA

^bDepartment of Radiology, University of Medicine and Dentistry of NJ, Newark, NJ 07101-1709, USA

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Abstract

Marshes have been proposed as sites for phytoremediation of metals. The fate of metals within plant tissues is a critical issue for effectiveness of this process. In this paper we review studies that investigate the effects of plants on metals in wetlands. While most of these marsh plant species are similar in metal uptake patterns and in concentrating metals primarily in roots, some species retain more of their metal burden in belowground structures than other species, which redistribute a greater proportion of metals into aboveground tissues, especially leaves. Storage in roots is most beneficial for phytostabilization of the metal contaminants, which are least available when concentrated below ground. Plants may alter the speciation of metals and may also suffer toxic effects as a result of accumulating them. Metals in leaves may be excreted through salt glands and thereby returned to the marsh environment. Metal concentrations of leaf and stem litter may become enriched in metals over time, due in part to cation adsorption or to incorporation of fine particles with adsorbed metals. Several studies suggest that metals in litter are available to deposit feeders and, thus, can enter estuarine food webs. Marshes, therefore, can be sources and well as sinks for metal contaminants. *Phragmites australis*, an invasive species in the northeast U.S. sequesters more metals belowground than the native *Spartina alterniflora*, which also releases more via leaf excretion. This information is important for the siting and use of wetlands for phytoremediation as well as for marsh restoration efforts.

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1. Introduction

Macrophytes have been shown to play important roles in marsh biogeochemistry through their active and passive circulation of elements. Through their action as “nutrient pumps” (Odum, 1988), active uptake of elements into plant tissue may promote immobilization in plant tissues, as seen in wetlands constructed for wastewater treatment (Kadlec and Knight, 1996) and in the use of wetland plants in phytoremediation. Phytoremediation is considered an effective, low cost, preferred cleanup option for moderately contaminated areas. Wetlands are often considered sinks for contaminants, and there are many cases in which wetland plants are utilized for removal of pollutants, including metals. The approach is generally one of “phytostabi-

lization”, where the plants are used to immobilize metals and store them below ground in roots and/or soil, in contrast to “phytoextraction” in which hyperaccumulators may be used to remove metals from the soil and concentrate them in aboveground tissues. These latter plants must be, in turn, harvested and disposed of to prevent recycling of accumulated metals when the plants decompose. However, with few exceptions (e.g. *Ceratophyllum demersum*, a freshwater submerged rooted species, that accumulates arsenic with a 20,000-fold concentration factor—Reay, 1972) wetland plants are generally not hyperaccumulators and, in any case, the mechanical aspects of harvesting plants would be destructive to wetlands comprised of rooted plants. Therefore, for wetland plants, storing metals below ground is the preferable alternative. While many engineering studies of treatment wetlands use a “black box” approach analyzing levels in the influent and effluent (for example, Cheng et al., 2002), more must be known about the patterns and processes of metal uptake, distribution and removal by different

* Corresponding author. Tel.: +1-973-353-5387; fax: +1-973-353-5518.

E-mail address: jweis@andromeda.rutgers.edu (J.S. Weis).

species of wetland plants. The extent of uptake and how metals are distributed within plants can have important effects on the residence time of metals in plants and in wetlands, and the potential release of metals. This information is needed in order to better understand these systems and to assure that the wetlands do not themselves eventually become sources of metal contamination to surrounding areas.

Senescent plant tissues may be sources of elements released through leaching and mineralization or can be sinks for elements through litter adsorption or microbial immobilization. The export of dead plant material that may be highly enriched in metals is a concern. Research on nutrients such as nitrogen (White and Howes, 1994) and phosphorus (Pomeroy, 1970) have demonstrated the importance of plant productivity, physiology and allocation patterns to salt marsh element cycles. Because plants also take up and process metals, these toxic contaminants may be released above surface through similar processes, thereby increasing their bioavailability in contaminated sites (Windom et al., 1976). Thus, for persistent materials such as metals, wetlands may be sources as well as sinks for contaminants. If metals are accumulated in aboveground tissues, they may pass on the contaminants to herbivores unless contaminated shoots are harvested. Since plant species can differ in rates of metal uptake, allocation and excretion, metal dynamics in salt marshes may be influenced by the composition of plant communities (Verkleij and Schat, 1990). When using wetlands for wastewater treatment or phytoremediation, one must be aware that the systems can sequester limited amounts and have an assimilative capacity that should not be exceeded without environmental damage.

In many tidal marshes of the eastern U.S., *Phragmites australis* Cav. Trin. ex Steud. (common reed) has been expanding over the past century from high marsh habitats into lower marshes, replacing *Spartina alterniflora* Loisel (salt marsh cordgrass). *P. australis* most easily invades sites considered “disturbed”, including wetlands constructed for mitigation purposes to offset the loss of natural wetlands (Havens et al., 2003). Because *P. australis* is physiologically and morphologically different from *Spartina* spp., its expansion can alter edaphic conditions (Windham and Lathrop, 1999; Bart and Hartman, 2000) and nutrient cycling processes (Windham, 1999; Meyerson et al., 2000). Despite studies that demonstrate its ability to maintain ecological functions in salt marshes (Warren et al., 2001; Windham, 1999; Rooth and Stevenson, 2000; Weis et al., 2002), wetland restoration projects frequently continue to remove *P. australis* and replant *Spartina* spp.

In this paper we have two goals: one is to review studies of metal dynamics in marsh plants in general. A second more specific goal is to compare metal dynamics in *P. australis* and *Spartina* species, two plants on which many studies have been performed. We review studies of metal uptake, distribution, toxicology, excretion from leaves and incorporation into detritus. While most studies have been on

either one or the other plant species and few studies have directly compared the two species, there are nevertheless differences that are apparent. These differences in metal distribution and release between the species have implications for metal dynamics in marshes, for wetlands as phytoremediation systems and for marsh restoration efforts.

2. Relations with sediments

Wetland sediments are generally considered a sink for metals and, in the anoxic zone, may contain very high concentrations of metals in a reduced state. As such, the bioavailability of the metals is low compared to terrestrial systems with oxidized soils. Different forms of metals have different availability: water-soluble metals and exchangeable metals are the most available, metals precipitated as inorganic compounds, metals complexed with large molecular weight humic materials and metals adsorbed to hydrous oxides are potentially available, and metals precipitated as insoluble sulfide and metals bound within the crystalline lattice of minerals are essentially unavailable (Gambrell, 1994). Because of these reducing conditions, the depth to which plant roots can penetrate is limited and this restricts the uptake of contaminants and rhizosphere actions to shallower levels (Williams, 2002).

In estuaries, much of the metal contaminants are bound to sulfides in anoxic sediments. However, plants can oxidize the sediments in the root zone through the movement of oxygen downwards through aerenchyma tissue (Moorhead and Reddy, 1988), and this oxidation can remobilize the metal contaminants, thus increasing the otherwise low availability of metals in wetland sediments. *Avicennia* species of mangroves were found to oxidize the rhizosphere, thus reducing sulfides and enhancing metal concentrations in the exchangeable form (De Lacerda et al., 1993). Metal remobilization may also result from acidification of the rhizosphere by plant exudates (Doyle and Otte, 1997). Wright and Otte (1999) found that *Typha latifolia* oxidized the rhizosphere, but this did not increase pore water metal concentrations. It caused decreased pH within 1 cm of the roots and increased the concentration of soluble zinc near and beneath the roots, while another plant, *Glyceria fluitans*, had little effect on sediment chemistry. Changes in sediment Eh and pH conditions can cause changes in metal speciation and solubility, which can result in a flux from sediments to porewater and then to overlying water and/or increase uptake into plants. It is possible that salinity changes may also alter metal speciation and uptake, but Drifmeyer and Redd (1981) found no correlation between salinity and metal content of *Spartina*. Lead uptake into roots and shoots of rice plants (*Oryza sativa*) decreased with an increase in redox potential and pH, while Cd uptake increased with an increase in redox potential and a decrease in pH (Reddy and Patrick, 1977). Greater uptake and availability of Cd was seen in a number of wetland species under dry (more

oxidized) than under flooded (reduced) conditions (Gambrell, 1994). The larger root system and increased number of fine roots of *S. alterniflora* compared with *P. australis* (Ravit et al., 2003) may indicate that the former species will oxidize the rhizosphere to a greater extent, increasing the availability of metals.

To complicate the situation, different forms (“species”) of the same metal can have different rates of uptake and different effects. For example, marsh sediments tended to reduce the very toxic Cr(VI) to the less toxic form, Cr(III), very rapidly (Pardue and Patrick, 1995). Many bacteria can methylate arsenic (Bentley and Chasteen, 2002) forming both volatile (e.g., methylarsines) and nonvolatile (e.g., methylarsonic acid and dimethylarsinic acid [DMAA]) compounds. Marine algae can transform arsenate into non-volatile methylated arsenic compounds (methanearsonic and dimethylarsinic acids) in seawater. This is considered to be a beneficial step not only to the primary producers, but also to the higher trophic levels, since non-volatile methylated arsenic is much less toxic to marine invertebrates. Freshwater algae like marine algae synthesize lipid-soluble arsenic compounds and do not produce volatile methylarsines. Aquatic plants also synthesize similar lipid-soluble arsenic compounds (Tamaki and Frankenberger, 1992). Submerged plants (*Ceratophyllum demersum* and *Elatine triandra*) in Canada accumulated arsenic, but mostly in organic form (methylarsonic acid and dimethylarsinic acid). Only a small proportion in the plants was inorganic arsenic, while most of the As in the surface water was as arsenate (Zheng et al., 2003). The availability of arsenic for uptake into *S. alter-*

niflora and *S. patens* varied with the species of arsenic, with DMAA having the lowest availability, followed by mono-methylarsonic acid (MMAA) and As(V), and with As(III) having the highest bioavailability. Inorganic arsenicals were mainly accumulated in the roots, while DMAA was readily translocated to the shoots (Carbonell-Barrachina et al., 1998).

A striking feature of roots of some wetland plants is the presence of metal-rich rhizoconcretions or plaque on the roots (Mendelssohn and Postek, 1982; Vale et al., 1990). These structures are composed mostly of iron hydroxides and other metals such as manganese that are mobilized and precipitated on the root surface. The metals are mobilized from the reduced anoxic estuarine sediments and concentrated in the oxidized microenvironment around the roots. Their concentrations can reach 5–10 times the concentrations seen in the surrounding sediments (Sundby et al., 1998). There have been conflicting reports as to whether the presence of the plaque reduces or increases the uptake of metal by the plants. The presence of these concretions appeared to reduce the amount of zinc taken up by *Aster tripolium* (Otte et al., 1989) and the amount of manganese taken up by *P. australis* (Fig. 1) (Batty et al., 2000). The mechanism may have been through the plaque acting as a physical barrier, although the barrier was not effective at low pH conditions. At higher pH conditions the presence of plaque enhanced Cu uptake into roots. However, in *T. latifolia* (cattail), the presence of iron plaque did not reduce uptake of toxic metals (Ye et al., 1998a). Iron plaque increased zinc uptake by rice (*O. sativa*) and movement

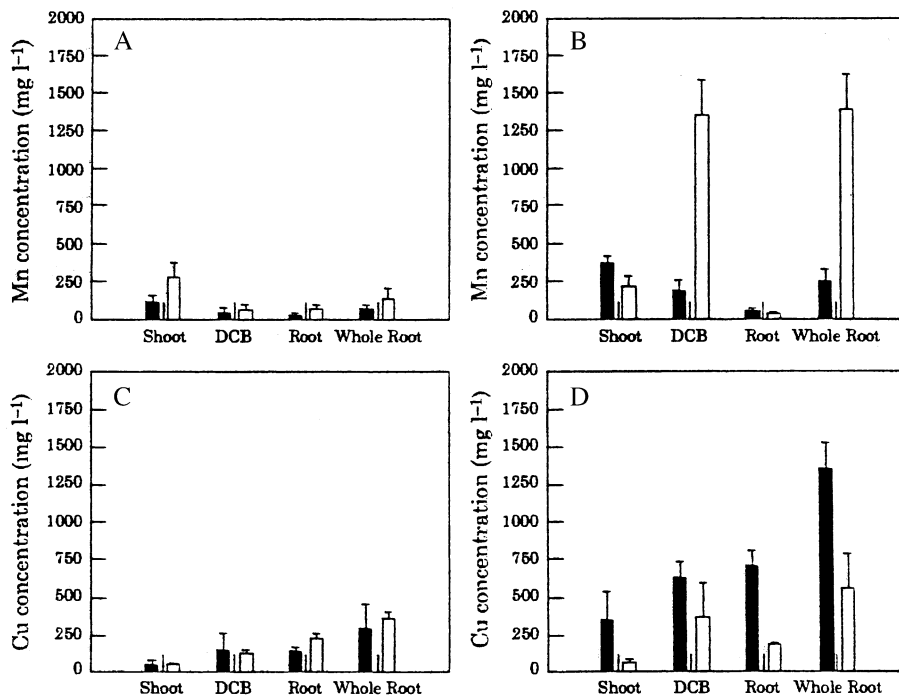


Fig. 1. Metal concentrations in *P. australis* seedlings exposed to 0.5 mg l⁻¹ Mn at pH 3.5 (A), 0.5 mg l⁻¹ Mn at pH 6.0 (B), 0.5 mg l⁻¹ Cu at pH 3.5 (C) and 0.5 mg l⁻¹ Cu at pH 6.0 (D) in the presence (black bars) or absence (white bars) of plaque. Reprinted from Batty et al. (2000), courtesy of Annals of Botany.

into shoots (Zhang et al., 1998). In contrast, Al was not adsorbed onto the iron or the manganese plaque but formed a separate phosphate deposit that resembled the iron and manganese plaques (Batty et al., 2002). They attributed the precipitate to the leakage of oxygen from the roots, and suggested that the phosphorus might be immobilized at the root surface. The discrepancies in effects of plaque on metal uptake need to be resolved by further study. Different metals, environmental conditions or physiologies may account for these differences.

By oxidizing the soil in the immediate vicinity of the rhizosphere, plants can alter the distribution of metals in wetland sediments. Doyle and Otte (1997) found that the concentrations of several metals were higher in vegetated

soils than in unvegetated ones, and were particularly high in soils in the immediate vicinity of the plant roots. In a study of cadmium and zinc concentrations in sediment cores from areas under *S. alterniflora* compared with adjacent mud flats without plant cover, the metal concentrations at 5–15 cm depth (corresponding to maximum root biomass) were higher by a factor of 4 under the vegetation (De Lacerda et al., 1997). Plant activity (metal mobilization by oxidation of the root zone and movement into the rhizosphere) was considered responsible for the increase. Similar results were found at sites with *S. maritima* by Caçador et al. (1996) (Fig. 2) who concluded that roots influence metal concentrations in the marsh sediments as a result of producing complex organic compounds and oxidizing the rhizosphere.

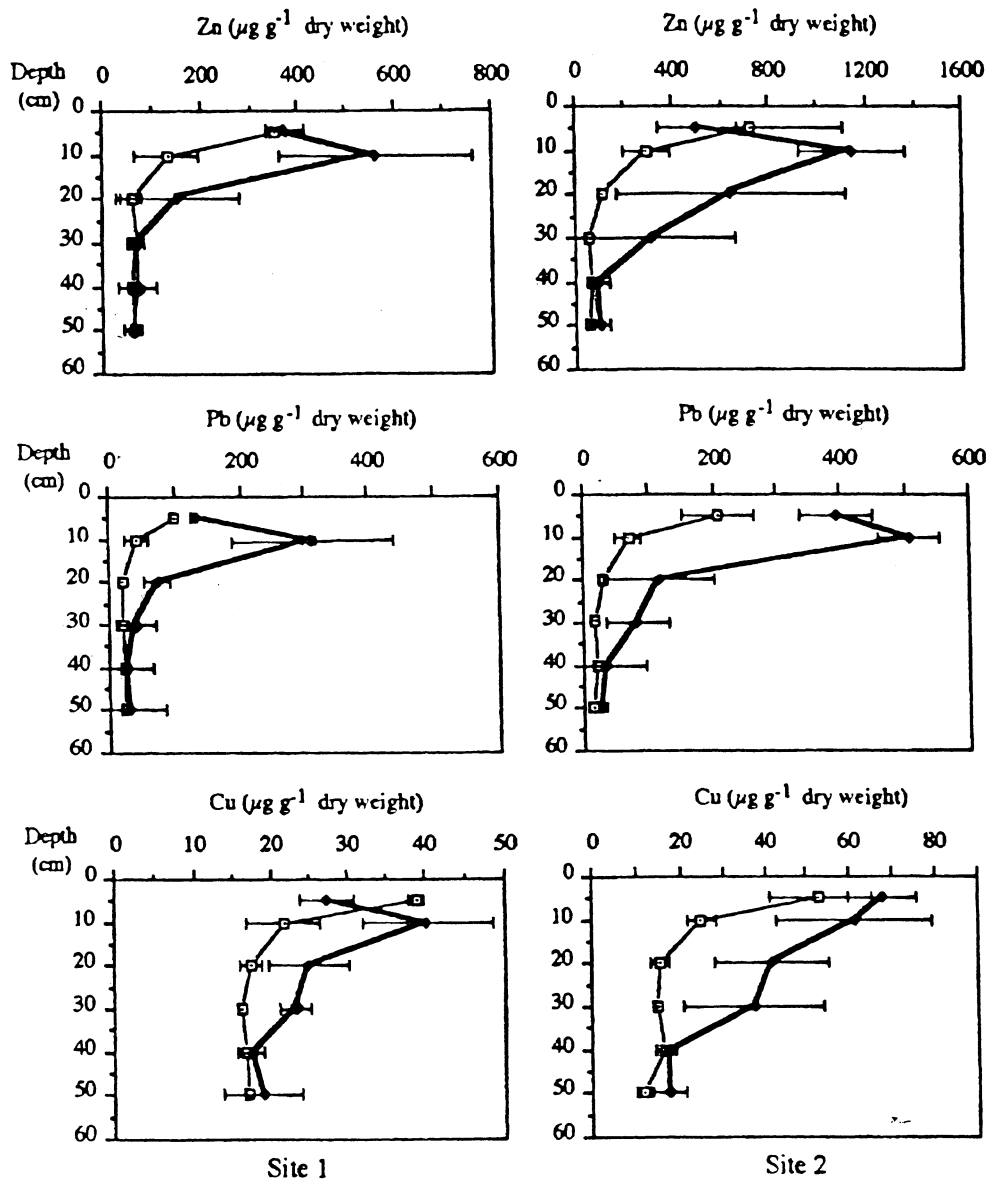


Fig. 2. Vertical profiles (mean \pm S.D., $n=3$) of total Zn, Pb and Cu concentrations ($\mu\text{g g}^{-1}$ dry weight) in sediment with (thick line) and without (thin line) vegetation from less contaminated site 1 and more contaminated site 2. Reprinted from Caçador et al. (1996), courtesy of Kluwer Academic Publishers.

3. Symbionts: bacteria, fungi and periphyton

Another factor that can affect the accumulation of metals in wetland plants is the presence of microbial symbionts such as rhizosphere bacteria. De Souza et al. (1999) found that, when bacteria were inhibited with antibiotics, plants (*Scirpus robustus* and *Polypogon monspeliensis*) accumulated lower concentrations of Se and Hg. Likewise, axenically grown plants that had bacteria added to them accumulated more of these metals than axenic controls, indicating an important role of these symbionts for efficient metal uptake (Fig. 3). Mycorrhizae (symbiotic fungi associated with roots) provide an interface between the roots and the soil increasing the absorptive surface area of root hairs and are effective at assimilating metals that may be present at toxic concentrations in the soil (Meharg and Cairney, 2000). Khan et al. (2000) suggested that they play a protective role, restricting the uptake of metals by plants by immobilizing the metals in the fungal tissue. However, there have also been reports of some plants accumulating higher metal concentrations, in some cases up to toxic levels, due to the presence of arbuscular mycorrhizae (Weissenhorn and Leyval, 1995). The presence of periphyton associated with *P. australis* in freshwater wetlands enhanced the ability of the reed to accumulate and retain metals (Lakatos et al., 1999). The relatively limited number of studies focusing on effects of symbionts on metal uptake suggests that it is one in need of greater attention in future studies.

4. Localization, translocation and distribution

4.1. Cellular localization

Metal concentrations analyzed in roots may reflect some proportion of metals that are merely adsorbed onto the root surface rather than within the root tissue. However, Vesk et

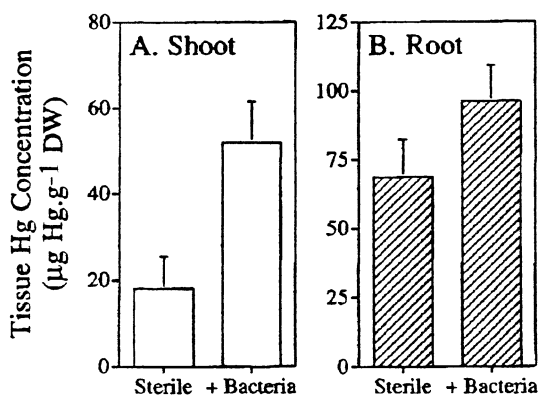


Fig. 3. Addition of a mixture of rhizosphere bacteria to axenic bulrush plants enhances Hg accumulation in tissues. Plants were supplied with 1 mg Hg l⁻¹. Means of three replicates are shown with their standard deviation. Reprinted from De Souza et al. (1999), courtesy of Springer-Verlag.

al. (1999) analyzed the localization of metals within roots of the water hyacinth (*Eichhornia crassipes*) using energy dispersive X-ray microanalysis, and found that copper, lead and zinc were not localized at the root surface, but were more highly concentrated in the inner root tissues. Levels were highest within cells of the stele (the vascular bundles), in electron-dense granules. Significant amounts were also seen in the cell walls. In the roots of seedlings of the grey mangrove, *Avicennia marina*, metals (Cu, Pb and Zn) were concentrated predominantly in cell walls (MacFarlane and Burchett, 2000). The root epidermis served as a barrier to transport of lead to aboveground tissues, but not the other metals. The endodermal casparian strip provided a barrier to the movement of all three metals into the stele. (This structure is a layer of impermeable waxy material, suberin and lignin in the walls of root endodermal cells that prevents passage of water and other molecules.) Once in the leaves, however, metals were highest in the xylem, followed by the mesophyll and then hypodermal tissue. Concentrations of metals in the cell walls were also higher than in intracellular locations.

4.2. Translocation to aboveground tissues

When wetland plants translocate metals from root tissue to aerial tissue, they are accumulated in leaves and stems. The degree of upward translocation is dependent on the species of plant, the particular metal and a number of environmental conditions. Fitzgerald et al. (2003) found that copper accumulated primarily in the roots of monocots and dicots, while lead accumulated mainly in the roots of monocots but in the shoots of dicots. For *A. tripolium*, lead accumulated mostly in the roots at low salinity, while at higher salinity a greater proportion of lead was translocated to the shoots. An inverse association of metals in the plants vs. in the sediments was noted for this species as well as *Spartina* spp., again suggesting plant uptake from the sediments.

Mangroves (species not specified) in Puerto Rico had much greater metal concentrations in “feeding roots” than in leaves except for manganese which was greater in leaves (Ragsdale and Thorhaug, 1980). Aerial roots had lower concentrations than feeding roots and woody tissue had the lowest concentrations. The grey mangrove, *A. marina*, accumulated metals in roots proportional to the concentrations in sediments. However, the degree of accumulation in leaves varied according to the metal. Accumulation of copper in leaves followed a linear relationship at lower concentrations then leveled off, indicating an exclusion mechanism operating at higher sediment levels (MacFarlane et al., 2003). Zinc accumulation in leaves correlated with sediment concentrations even when they were high, indicating the greatest translocation to aerial portions of the plant. However, lead levels in leaves remained quite low at all levels of sediment lead. Lower pH resulted in increased zinc accumulation, and higher levels of lead and zinc in the

sediments resulted in greater lead accumulation in roots and shoots. Cattails, *T. latifolia*, were also found to accumulate metals mostly in the roots (Ye et al., 1997b). However, seedlings from a population from a metal-contaminated environment accumulated more zinc, lead and cadmium in roots than seedlings from a reference population when both types of plants were grown in a common environment.

4.3. Comparison of *Spartina* and *Phragmites*

Cordgrass, *S. alterniflora* transports significant levels of metals to aboveground tissues (Banus et al., 1976; Giblin et al., 1980; Kraus et al., 1986; Kraus, 1987). Rahn (1973) suggested that *S. alterniflora* may be an efficient pathway of mercury transfer into the food chain, since it takes Hg up through the roots, transports it upwards and can export it in detritus. Breteler and Teal (1981) found that concentrations of mercury in *S. alterniflora* biomass increased when growing in mercury-contaminated sediment (amended with sewage sludge) but determined that most of the mercury was in root tissue. Alberts et al. (1990), however, investigated metals in sediments and in both above-ground and below-ground tissue of *S. alterniflora* collected from a large number of contaminated and reference marsh systems in Georgia; in contrast to the findings of Breteler and Teal (1981), they found comparable concentrations of copper and mercury in above-ground and below-ground tissues, while aluminum, iron and zinc were greater in below-ground tissues. They concluded that the internal concentrations of metals were controlled by the plant. *S. cynosuroides* from a

single site showed more highly variable metal concentrations in tissues. Newell et al. (1982) investigated a formerly mercury-contaminated site 10 years after it was cleaned up and found that concentrations of mercury remained high in leaf tissues of *S. alterniflora*. However, other metals that had previously been high no longer showed elevated levels in leaves after this amount of time.

In a study of arsenic accumulation and toxic effects in *S. alterniflora*, Carbonell et al. (1998) found that the form of arsenic was a critical factor, with inorganic arsenicals and MMAA being mainly accumulated in the roots, while DMAA was more readily transported to the shoots. In a study in hydroponic conditions, Carbonell-Barrachina et al. (1998) found a similar pattern, but also stated that regardless of the chemical form of arsenic both root and shoot concentrations significantly increased with increased levels of As in the medium.

High levels of metals (copper, lead and zinc) were found in aboveground tissues of *S. maritima* in a contaminated estuary in Spain (Luque et al., 1999). Plants in the low marsh had higher levels than those in the high marsh, and old leaves had higher concentrations than young leaves. The authors concluded that the plants play an important role in the transfer of metals through estuarine food webs. Differences in metal accumulation between the short (higher marsh, asexual) form and tall (low marsh, sexually reproducing) form of *S. alterniflora* were noted by Ornes et al. (1998). While zinc and copper were higher in the short form than the tall form, there were no seasonal differences observed.

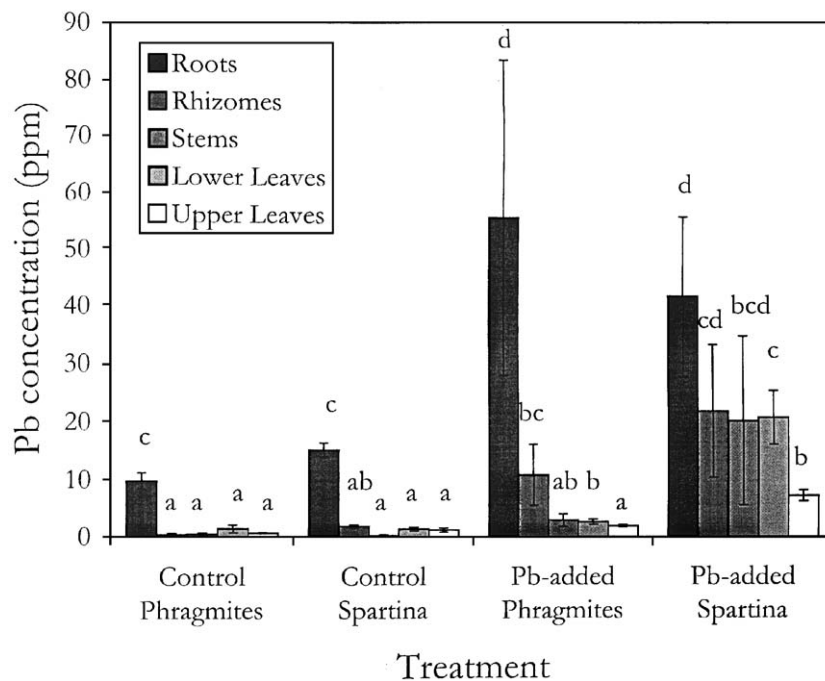


Fig. 4. Concentration of lead in individual tissues of each species grown in each Pb treatment. Error bars = S.E. Alphanumeric characters denote results of Fisher's LSD post-hoc tests. Reprinted from Windham et al. (2001b), courtesy of Elsevier Publishing.

P. australis is widely used in constructed wetlands for treatment of wastewaters that contain metals. *P. australis* is known to take up metals from sediments, but compared to *S. alterniflora* it concentrates a greater proportion of its body-burden of metals in root and rhizome tissue, translocating smaller amounts to above-ground tissues. Kraus (1987) reported that, in plants collected from the same contaminated site in the Hackensack Meadowlands, NJ, *P. australis* had higher root concentrations of Ni, Cd and Pb than *S. alterniflora*. Stem levels of the metals were higher in *S. alterniflora*, and leaf levels were comparable in the two plants. Keller et al. (1998) suggested that only minor amounts of metals are moved up from roots to above-ground tissues by *P. australis*, although Schierup and Larsen (1981) found high concentrations of Zn above-ground, while other metals were retained in the roots and rhizomes. Peverly et al. (1995) studied a constructed marsh receiving landfill leachate and found that most metals (copper, lead, cadmium and iron) accumulated only within roots, although zinc did accumulate in shoots. They stated that the roots were remarkably effective at restricting flow into vascular tissue, thereby restricting upward transport of the metals. In marked contrast to previous studies, Fitzgerald et al. (2003) found that *P. australis* in Ireland translocated more copper and lead upward to shoots than did *Spartina* spp.

Ye et al. (1997a) compared different populations of *P. australis*, one from a contaminated mine site and three from clean sites, and found similar metal uptake of zinc, lead and cadmium. Thus, there was no evidence found that the metal-contaminated population modified its uptake or distribution of metals as a response to living in a contaminated environment, and translocation of metals to the shoots was minimal in all populations. In a follow-up study they found

that metals were taken up more rapidly during flooded rather than dry conditions in all populations (Ye et al., 1998b).

In a greenhouse study of *S. alterniflora* and *P. australis* grown in sediments to which lead had been added (Windham et al., 2001b), concentrations of lead were greater in *S. alterniflora* leaves and rhizomes (Fig. 4) than in those of *P. australis*. Upper, i.e., younger, leaves had lower lead concentrations than lower leaves for both species of plants. Pools of lead in aboveground biomass were 40% greater in *S. alterniflora* than in *P. australis*, while pools of lead belowground were not statistically different between the two plant species (Fig. 5). *P. australis* had a much lower ratio of leaf/stem pools (2.8 vs. 25.6, respectively), indicating a much greater restriction on the allocation of lead aboveground into photosynthetic tissue.

Thus, in studies comparing the two species, *P. australis* appears to have a tighter restriction on upward movement of metals, while *S. alterniflora* transports greater amounts to aboveground tissues, especially leaves.

5. Seasonal distribution

Seasonal variations in metal levels have been noted in a number of species, but they are not necessarily consistent with each other. Some reasons for these discrepancies may include the choice of which leaves are selected for analysis. Weis et al. (2003) have found great variation among leaves within the same plant at any given time of sampling, so that results could be very different depending on which leaves were selected. This suggests that it is important to analyze a large number of leaves and not assume that a few are representative of the plant as a whole.

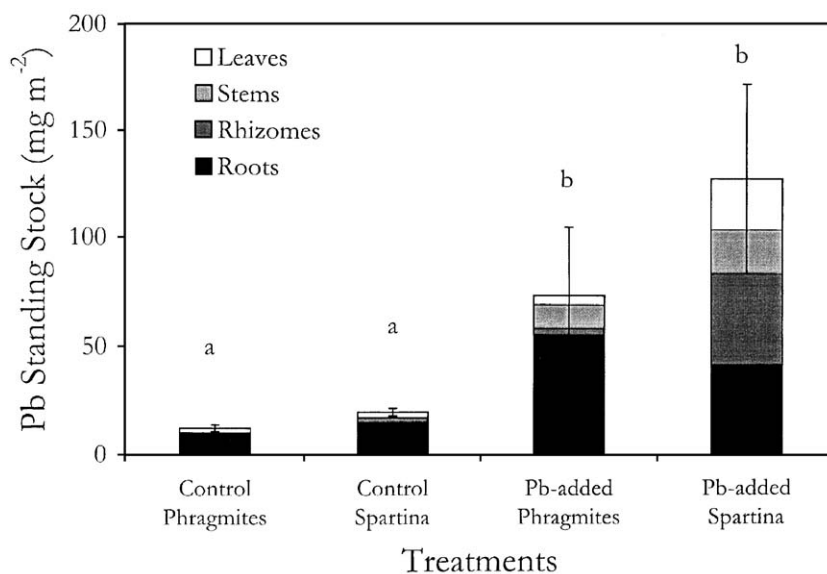


Fig. 5. Standing stock of lead in whole plants and individual tissues of each species grown in each Pb treatment. Error bars = 1 S.E. for whole plant standing stock of Pb. For legend, see that of Fig. 3. Reprinted from Windham et al. (2001b), courtesy of Elsevier Publishing.

Seasonal variations were noted by Caçador et al. (2000) in root concentrations of zinc, lead, copper and cadmium in *S. maritima* and *Halimone portulacoides*. The lowest levels in roots were in January and they increased during the growth period, suggesting that plant activities were responsible for the uptake. Sediment concentrations of these metals were lowest when root levels were highest, suggesting plant uptake from the sediments.

Ragsdale and Thorhaug (1980) noted in several salt marsh plant species as well as the submerged sea grasses *Zostera marina* (eel grass) and *Thalassia testudinum* (turtle grass) that Cd, Cr and Mn increased at the end of the growing season when plants senesced, while Pb, Zn and Cu remained relatively constant. Mercury concentrations in *Posidonia oceanica* leaves were higher in the winter than the summer, thus showing a negative correlation with the plant's phenology (Capiomont et al., 2000). Also, concentrations were lower in young tissue than in older tissues, consistent with other studies. The lowest levels were found in the sheaths. In *S. alterniflora*, however, shoots accumulated manganese, copper and zinc rapidly in the spring and then the levels declined (Gleason et al., 1979). The decline was attributed to a growth dilution effect. Metal levels in *A. triplolium*, *Puccinellia maritima* and *Spartina anglica* were also high in the spring and declined in the summer and autumn (Leendertse et al., 1996). In contrast, Ornes et al. (1998) found no seasonal changes in zinc or copper levels in *S. alterniflora* in South Carolina, while manganese did show seasonal changes, being lowest during the spring and summer. Concentrations of zinc, lead, copper and cadmium in roots of *S. maritima* were found to vary seasonally, with low levels in the winter and increasing levels during the spring and summer growth period (Caçador et al., 2000). A decrease in mercury in *S. alterniflora* leaves from May to July was noted by Heller and Weber (1998). Drifmeyer and Redd (1981) noted that standing dead leaves had higher metal concentrations of manganese, iron, copper, zinc and nickel than leaves of live plants.

In a study of seasonal distribution, Larsen and Schierup (1981) found that zinc in leaves and stems of *P. australis* from a freshwater lake was at a maximum during the growth season and then decreased, while copper in leaves remained relatively constant. In contrast, lead in leaves showed a sharp increase during and after the growth season. Schierup and Larsen (1981) found that leaves produced earlier in the growing season had higher concentrations of Hg than leaves produced later. They hypothesized that this may be due to the age of leaves, such that newly expanding leaves are low in metals and as they photosynthesize over the growing season, they gradually accumulate more metals until senescence. Metal concentrations, therefore, may rise as leaves age simply due to the continued passive transport of metals into leaf tissues. Luque et al. (1999) also found that old leaves had higher concentrations of various metals than young leaves; this may have been due to the early leaves being provided with more metals from the beginning or to

continued deposition of metals into given leaves over time. Weis et al. (2003) demonstrated that metal (copper, lead and zinc) concentrations in individual leaves of both *S. alterniflora* and *P. australis* did increase greatly from the time the leaf was new until it was senescent. Movement of metals into aging leaves is a way for plants to eliminate some of their metal burden (Verkleij and Schat, 1990).

Comparative studies of metal uptake and distribution in *S. alterniflora* and *P. australis* were reported by Windham et al. (2003) for a field study over a growing season. Both metal concentrations and standing stocks (concentration \times biomass) in the two species of plants were analyzed. In the study at a contaminated salt marsh in the Hackensack Meadowlands in northern New Jersey where the two species were growing intermingled, both species had the highest concentrations of all metals in the roots. For mercury and chromium in leaves, concentrations were greater in *S. alterniflora* than *P. australis* from April to October. Leaf concentrations of the other three metals examined (copper, lead and zinc) were more variable between species throughout the season. For *P. australis* leaf tissue, metals declined over the summer, with zinc and copper concentrations rebounding in senescent leaf tissue in October. For *S. alterniflora* leaf tissue, mercury and copper concentrations declined over the sampling period, but chromium and zinc increased during the summer then declined in October. Metal pools, when considered as standing stocks at the whole plant scale, did not show clear seasonal patterns. However, standing stocks of mercury and chromium in leaf tissues were greater in *S. alterniflora* than in *P. australis* from April through August, while copper and zinc were greater in *P. australis* leaves in August and October. For *S. alterniflora*, 50–80% of the aboveground pool of all metals examined was found in leaf tissue, whereas in *P. australis*, which has a higher proportion of stem tissue, only 4–20% of the aboveground metals was found in leaf tissue.

It is difficult to generalize about seasonal changes in metal levels, since they appear to vary greatly with the metal and the species of plant studied. One factor that does seem fairly constant, however, is that individual leaves acquire greater concentrations of metals over their life span.

6. Plants and metal speciation

There have been few studies on plants altering the speciation of metals. *S. alterniflora* was found to convert selenium to DMSeP (dimethylselenoniopropionate), a non-toxic form that can be volatilized (Ansedé et al., 1999). Windom et al. (1976) found no evidence that *S. alterniflora* in Georgia was involved in methylating mercury or accumulating this organic and more toxic form of Hg. However, Heller and Weber (1998) found that this form of Hg was present in *S. alterniflora*. While concentrations of

inorganic mercury decreased throughout the growing season of *S. alterniflora* in a New England salt marsh, the percent of the total mercury that was the highly toxic methylmercury increased from May to July (up to 48%), and then decreased in October (Fig. 6). They speculated that either the plant is capable of methylating Hg, or there is a selective uptake from sediments in which the mercury is typically 1–3% methylated. In either case, the process appears to be accentuated by warmer weather. Roots of floating macrophytes such as the water hyacinth have been found to be sites of active methylation of mercury (Mauro et al., 1999). Up to 35% of added mercury was methylated and rates were higher at higher temperature. The methylation was attributed to sulfate-reducing bacteria associated with the roots. Guimaraes et al. (2000) found that roots of the freshwater macrophytes *Eichhornia azurea*, *E. crassipes*, *Paspalum* sp., *Eleocharis sellowiana*, *Salvinia* sp., *S. rotundifolia* and *Scirpus cubensis* had an order of magnitude higher level of methylation in their roots than the underlying lake sediments. The methylation was attributed to microorganisms attached to the roots and associated solids, rather than the roots themselves. Root exudates were considered a source for carbon to stimulate bacterial activity. Fine lateral roots of the water hyacinth, *E. crassipes*, were also found to reduce the highly toxic Cr(VI) to the less toxic Cr(III), then translocate the relatively non-toxic Cr(III) to leaf tissues (Lytle et al., 1998). This plant-induced transformation, unlike that of mercury, could be used in detoxification of contaminated waste streams. On the other hand, it has been proposed that phytoremediation projects for mercury-contaminated sites utilize plants genetically engineered with the bacterial mercury-resistance genes “merA” and “merB” to remove mercury by converting mercury salts and methylmercury to the volatile Hg(0), which would be released into the atmosphere (Heaton et al., 1998). These papers do not consider potential negative effects when this atmospheric mercury gets deposited elsewhere.

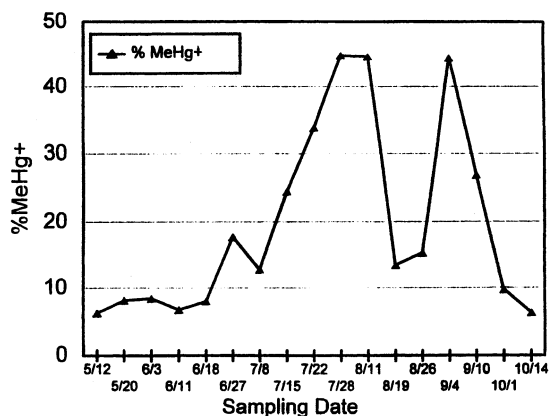


Fig. 6. Percent methylmercury of total Hg vs. sampling date in *S. alterniflora* from Chapman's Marsh during the 1997 growing season. Reprinted from Heller and Weber (1998), courtesy of Elsevier Publishing.

7. Toxicological effects

Metals accumulated in plant tissues can cause toxic effects, especially when translocated to above ground tissues. Effects can be measured at the biochemical and cellular level, but most studies of effects have focused on growth as the response to the toxicant. Grey mangroves seedlings, *A. marina*, when exposed to 100 $\mu\text{g/g}$ sediment copper showed a significant reduction in seedling height, leaf number and leaf area (MacFarlane and Burchett, 2002). At 400 $\mu\text{g/g}$, a decrease in total biomass and root growth were observed. Emergence was totally inhibited at 800 $\mu\text{g/g}$. In contrast, very little lead was translocated to aboveground tissues and minimal negative effects were observed. Zinc was translocated to leaves and at 1000 $\mu\text{g/g}$ sediment zinc all seedlings died. Significant reductions in height, leaf number, area, biomass and root growth were seen at 500 $\mu\text{g/g}$ sediment zinc. There was an additive interaction of the zinc and lead when both were present.

7.1. Effects at the biochemical or physiological level

A number of physiological indices of effect in *Spartina maritima* were studied by Padinha et al. (2000). Thiolic protein concentration, adenylate energy charge (AEC) and photosynthetic efficiency were measured in plants growing at sites with differing degrees of metal contamination. Thiolic protein (which binds metals) was higher in plants growing in metal-contaminated environments, while leaf AEC ratio and photosynthetic efficiencies were lower in plants from the polluted sites. Metals bound to thiolic proteins were subsequently excreted back to the environment, maintaining lower concentrations in the leaves. The production of these proteins was thus a mechanism for elimination of the metals. These indices, reflecting toxic responses, were considered to be useful for quantifying health of the plants and could potentially be used as biomarkers. Mendelssohn et al. (2001) also examined physiological indicators in *Typha domingensis* and *S. alterniflora* in response to increasing levels of cadmium. Leaf expansion, the live/total ratio of aboveground biomass and the regrowth after initial harvest were significantly reduced with increased cadmium (Fig. 7). Of the physiological indicators (photosynthesis, chlorophyll fluorescence, AEC ratio and leaf reflectance) only photosynthesis (Fig. 8) and AEC ratio responded to cadmium before damage was visible, and were thus the two most sensitive indices. Chlorophyll fluorescence was relatively insensitive.

The form of arsenic was found to affect its toxicity to *Spartina patens* (Carbonell et al., 1998). DMAA was the most phytotoxic, while As(V) and MMAA increased plant growth at low concentrations, which was associated with increased plant phosphorus. The organic arsenicals decreased root concentrations of copper, iron and manganese

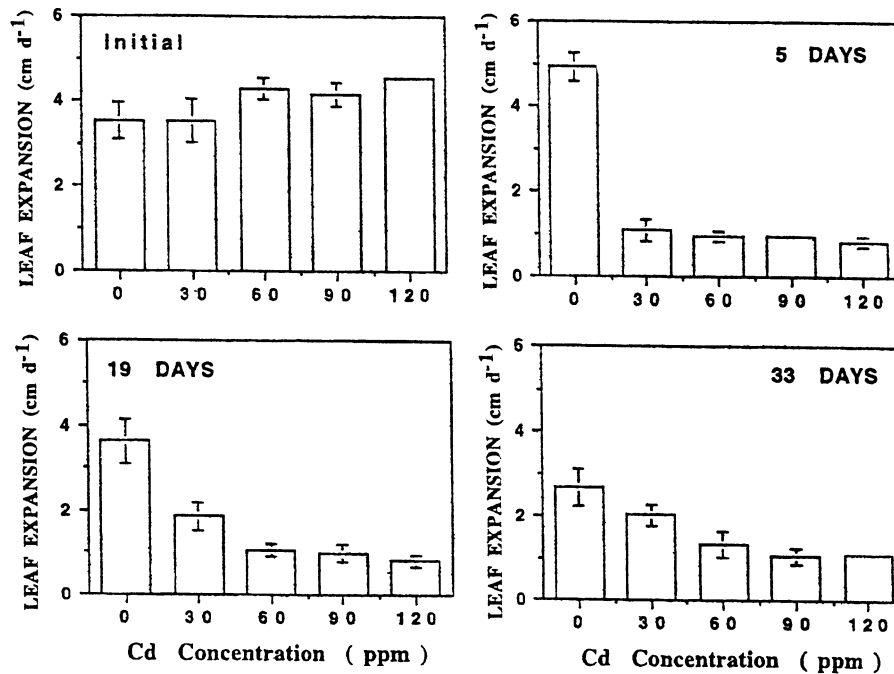


Fig. 7. Leaf expansion rates measured in *S. alterniflora* prior to (initial) and 5, 19 and 33 days after application of CdCl_2 . Treatment levels are expressed as 0, 30, 60, 90 and 120 ppm Cd. Reprinted from Mendelsohn et al. (2001), courtesy of Elsevier Publishing.

and shoot concentrations of boron and copper. The toxicity of DMAA appeared to be associated with reductions in essential nutrients (phosphorus, potassium, calcium and magnesium) and micronutrients (boron, copper, iron and manganese). More studies on biochemical and physiological responses are needed.

7.2. Studies of metal tolerance

Ye et al. (1997a, 1998b) used growth as a measure of response of *P. australis* seedlings to zinc, cadmium and lead in order to compare a population from a mine site with a reference population to investigate if tolerance had been

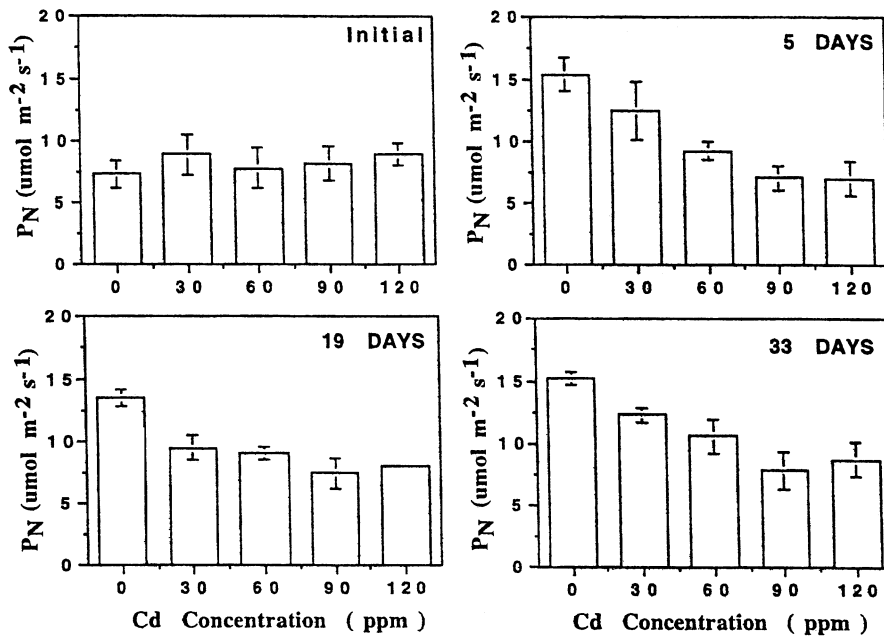


Fig. 8. Net photosynthesis (PN) rates in *S. alterniflora* prior to (initial) and 5, 19 and 33 days after application of CdCl_2 . Treatment levels are expressed as 0, 30, 60, 90 and 120 ppm Cd. Reprinted from Mendelsohn et al. (2001), courtesy of Elsevier Publishing.

acquired by the contaminated population. Both populations were found to be very resistant to toxic effects and no enhanced tolerance of the polluted population was noted. This finding indicated that if this species were to be used in constructed wetlands, it would not be necessary to select a particular resistant population. Hronec and Hajduk (1998) also remarked on the high resistance of *P. australis* to magnesium-contaminated soils in mining areas and felt the species would be useful in reclamation projects. In studying *T. latifolia*, however, Ye et al. (1997b) found that seedlings from contaminated sites accumulated more metals in roots than plants from uncontaminated areas, although the tolerance to metals was comparable in both the polluted and the unpolluted populations. There is need for more studies of tolerance in other species of wetland plants.

Tolerance to metals in plants can be achieved by sequestering them in tissues or cellular compartments (e.g. central vacuoles) that are insensitive to metals. Restriction of upward movement into shoots (an avoidance mechanism) and the translocation of excessive metals into old leaves shortly before their shedding can also be considered tolerance mechanisms, as can the increase in metal-binding capacity of the cell wall (Verkleij and Schat, 1990). A common biochemical biomarker in plants is the presence of phytochelatins, peptides (polycystein) that are synthesized rapidly in plant tissues after metal exposure and serve to chelate them (Grill et al., 1985). When all free metal ions are chelated, synthesis is terminated. The lower amount of free metals in the cells allows metal-sensitive enzymes to function and the plant to survive. The capacity for chelation is finite, however, and as metal concentrations continue to increase, toxic effects become manifested (Sneller et al., 1999). Other metal-chelating substances may be present in plant exudates, which act to decrease metal uptake, and consequently toxicity (Verkleij and Schat, 1990).

8. Metal release by leaves

The release of metals from leaf tissues onto the leaf surface is a method for dealing with metals, the relative importance of which varies with the physiology of individual plant species. Metal release by plants can increase the bioavailability of metals within estuaries, especially in urban and industrialized areas, where even small releases from contaminated sites can have toxic effects on estuarine food webs (Berk and Colwell, 1981). Leaves of seedlings of the mangrove *A. marina* excreted significant quantities of zinc or copper after exposure to these metals (Waisel, 1977; MacFarlane and Burchett, 2000). The metals were associated with salt crystals excreted on the adaxial leaf surface. Likewise, *S. alterniflora* has been shown to actively excrete metals in salt crystals released through hydathodes (salt glands) (Kraus et al., 1986; Kraus, 1988). Kraus (1988) estimated that *S. alterniflora* has the theoretical potential to export 145 g cadmium, 260 g lead, 104 g chromium, 260 g

copper and 988 g nickel per ha/year through salt excretion. The relationship of metal release with salt excretion suggests that there will be greater metal release at higher salinities, when there is more salt excretion. This is an area deserving of further research.

In a contaminated area of the Hackensack Meadowlands in northern New Jersey, leaf excretion by *S. alterniflora* and *P. australis* growing together in the same sediment was studied. Leaves of *S. alterniflora* were found to release two to four times more lead, copper, chromium and zinc than leaves of *P. australis* at the peak of the growing season (Burke et al., 2000). Leaf concentrations of copper and zinc were comparable in leaves of the two species, while *S. alterniflora* had higher leaf concentrations of lead and chromium. Thus, *S. alterniflora* can release larger quantities of metals into the marsh environment than *P. australis*. Differences in metal release between the two plant species may be due to the presence of salt glands in *S. alterniflora* which are absent in *P. australis*. Environmental conditions are likely to influence rates of metal release from these species. Windham et al. (2001a) examined mercury release from leaves of the two species, growing together at the same site throughout 3 months of the growing season. Similar to the other metals, the rate of mercury release from leaf tissue was two- to three-fold greater for *S. alterniflora* than for *P. australis* (Fig. 9). Rates of mercury release were highest for both species in late May, followed by lower rates in late June and July. Concentrations of mercury in the leaves followed a similar pattern, with higher leaf Hg concentrations in May than in June or July, similar to that reported by Heller and Weber (1998). Sodium release was consistently greater in *S. alterniflora* leaves, and transpiration rates were consistently greater in *P. australis* leaves. Transpiration rates were not correlated with mercury release in either species.

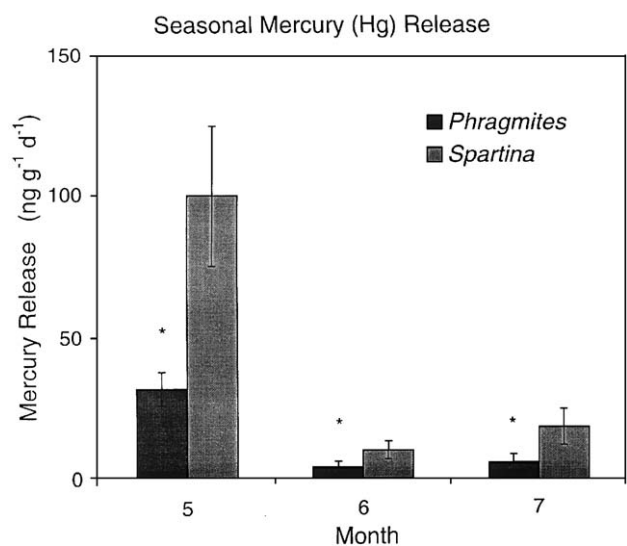


Fig. 9. Hg release from leaf tissue of *S. alterniflora* and *P. australis* from May–July. Error bars denote 2 S.E. Reprinted from Windham et al. (2001a), courtesy of Estuarine Research Federation.

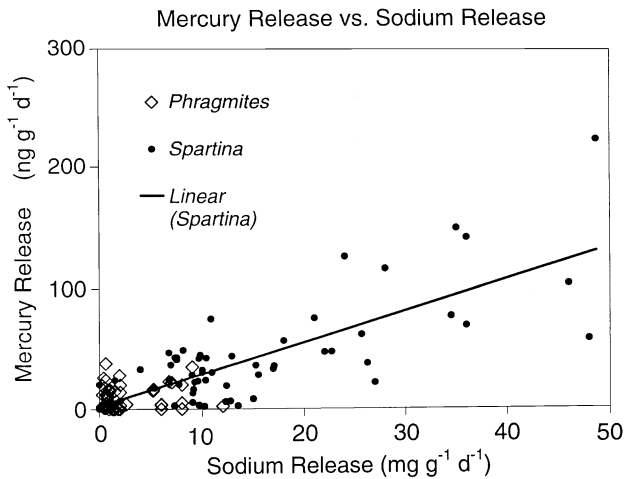


Fig. 10. Relationship of Hg release to Na release in *S. alterniflora* and *P. australis*. Significant result for *S. alterniflora* only ($r^2=0.210$). Regression equation: $\log \text{Hg release} = 0.126 + 1.019 * \log \text{Na release}$. Reprinted from Windham et al. (2001a), courtesy of Estuarine Research Federation.

Rates of sodium release were correlated with mercury release for *S. alterniflora* but not for *P. australis* (Fig. 10), which is consistent with the excretion of the metals via the salt glands of *S. alterniflora*. Hg release was strongly correlated with leaf concentration of mercury for both species, but the slope of mercury release to leaf mercury concentration was greater for *S. alterniflora* during all months. Therefore, for a given leaf level of mercury, more was released from *S. alterniflora* than from *P. australis*.

9. Metal export via detritus

Metals in aboveground tissues are likely to remain when these tissues die and turn into detritus. Metals stored in aboveground portions of plants that die, decay and turn into detritus, may become available to deposit feeders, and consumption of metal-laden detritus can cause deleterious effects in consumers (Dorgelo et al., 1995). Metals may also leach out of detritus to reenter the estuarine water. Generally concentrations of metals increase in standing dead plant biomass and in detritus. The development of a microbial community in the decaying litter tends to facilitate increases in metals through the active metabolism of the microbiota. A number of studies have focused on metal enrichment in decaying litter over time. Concentrations of Fe, Cr, Cu, Pb and Mn increased in litter of the seagrass *T. testudinum*, while Zn concentrations did not change and Cd concentrations declined (Ragsdale and Thorhaug, 1980). Litter of the grey mangrove, *A. marina*, became enriched with lead (MacFarlane et al., 2003). Increasing levels of lead in sediments and a decrease in sediment pH led to increased levels in the litter. However, copper and zinc levels in litter were not associated with sediment levels of copper and zinc. Copper levels in litter tended to be lower than levels in the

original leaves, in which levels tended to increase during senescence. Since *S. alterniflora* stores more of the toxic mercury and chromium in aboveground biomass, it is likely to release more of these toxicants into food webs than *P. australis*, while the latter plant may release more of the micronutrients copper and zinc. In addition, aboveground metals in *S. alterniflora* are primarily in leaves, which are more easily degraded by decomposers and weathering than stems and, therefore, are probably more likely to release more of the metals before being buried under newly deposited sediment. Studies have demonstrated that *S. alterniflora* retains metals in standing dead leaves and in detritus (Kraus et al., 1986; Sanders and Osman, 1985). Giblin et al. (1980) found that the litter of *S. alterniflora* became enriched in copper as decomposition proceeded. They found that chromium and zinc also accumulated in litter, but were later desorbed from the litter. They speculated that the litter might function as a cation exchanger, absorbing ions from the sediments. They also found that detritus-feeding animals (e.g. fiddler crabs—*Uca* spp.) took up the metals from the detritus. Drifmeyer et al. (1982) found that much of the metals bound on *S. alterniflora* detritus were easily desorbed, suggesting they were readily bioavailable to detritus feeders.

Substantial increases in mercury, copper, iron and zinc concentrations in decomposing *S. alterniflora* detritus were observed by Breteler and Teal (1981). These increases were greater than could be accounted for by the loss of plant material concentrating the metals, and the authors considered the increases to be a result of adsorption of metals from the sediments. In contrast to the gradual increase in metals over time seen in the previous studies, decaying litter of *S. foliosa* was found to undergo a very rapid increase in all metals during the first few weeks of decomposition, followed by a subsequent slower increase (Zawislanski et al., 2001). Accumulation of fine particulate matter in the litter was considered to be the major mechanism for the enrichment, rather than adsorption from the sediments.

Decomposition studies on litter of *P. australis* have also indicated enrichment in metals over time. Larsen and Schierup (1981) found that the concentrations of zinc, copper, lead and cadmium increased significantly during decomposition. The actual contents (pools) of zinc and copper were relatively constant or else decreased over time, suggesting loss of plant biomass causing metals to become more concentrated, and leaching of these metals, while the contents of lead and cadmium increased, suggesting that these metals are actively accumulated into the decomposing material.

Studies on metal accumulation in litterbags containing either leaves or stems of either *S. alterniflora* or *P. australis* indicated that the site of decomposition and the tissue type were more important than the species of plant in determining the metal uptake in the litter (Windham et al., 2002). Decaying leaves accumulated greater amounts than stems. Initial species and site differences in metal levels in dead

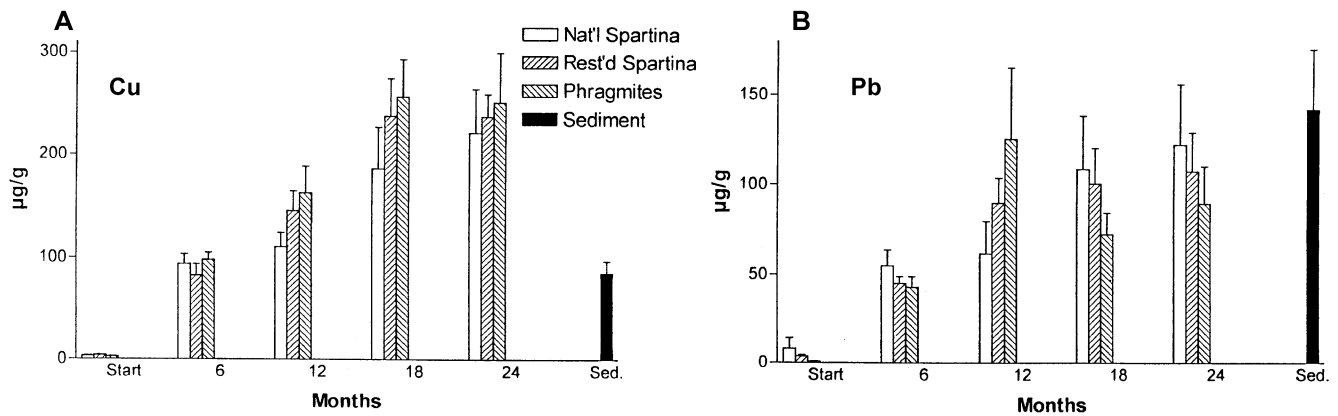


Fig. 11. Accumulation of Cu and Pb in litter of *S. alterniflora* (natural and restored) and *P. australis* over a 2-year period in relation to the sediment metal concentration at the site. From Windham et al. (2002).

leaves were rapidly obliterated as the metals accumulated in the litter (Fig. 11). Metals became more enriched in the litter decaying at a site where the sediment concentrations were lower than a second site at which the litter did not become as enriched. This is reminiscent of the findings of MacFarlane et al. (2003) who found that levels of copper and zinc in mangrove leaf litter were not associated with sediment copper and zinc levels. At the first site, levels of copper and zinc in the litter after 1 year exceeded the levels in the surrounding sediments, suggesting active uptake (by the microbial community) rather than passive adsorption onto the litter. This site had a lower pH and higher salinity than the second site at which litter did not become as enriched; these environmental factors may have played a role in the differential metal accumulation at the two sites.

Thus, despite differences in mechanisms of accumulation, there is a general pattern that decaying litter of marsh plants becomes enriched in metals over time. This suggests that the litter would become more hazardous to detritus feeders, provided that the metals contained in the litter are available.

10. Conclusions

Are marshes sources or sinks for metals? It is often stated that wetlands serve as sinks for pollutants, reducing contamination of surrounding ecosystems. While sediments, which tend to be anoxic and reduced, act as sinks, the marsh can become a source of metal contaminants through the activities of the plant species. Plants can oxidize the sediments making the metals more bioavailable. Metals can be taken up by roots, transported upward to above-ground tissues, from which they can be excreted. Decaying litter can accumulate more metals, which may leach or may become available to detritus feeders. Using wetlands for water purification may serve only to delay the process of releasing toxicants to the water. As levels of pollutants increase, the ability of a wetland system to incorporate

wastes can be impaired and the wetland can become a source of toxicity.

Overall, Leendertse et al. (1996) found that about 50% of the absorbed metals were retained in salt marshes and 50% was lost (exported). Despite the possibility of plants mobilizing metals, the overall effects of plants on metal biogeochemistry and mobility suggested to Jacob and Otte (2003) that wetlands nevertheless generally act as sinks rather than sources for metals when considered over a long term. Likewise, MacFarlane et al. (2003) conclude that mangrove communities are effective traps for immobilizing heavy metals, with relatively low export to adjacent ecosystems. However, since many wetland plants, unlike mangroves, are relatively short lived, their ability to stabilize metals may be only for the short-term.

Different plant species have different allocation patterns of metals and can have different effects on salt marsh ecosystems. Based on the studies reviewed here, the replacement of *S. alterniflora* by invading *P. australis* would be predicted to lead to a reduction in mercury, chromium and lead bioavailability, due to the higher allocation of these metals to leaf tissues in *S. alterniflora*. For a given metal burden, *P. australis* allocates more of the metal pool into both belowground biomass, and recalcitrant tissues (stems, rhizomes, roots) than *S. alterniflora*. Furthermore, the excretion of metals by leaves is also greater for *S. alterniflora* than for *P. australis*, probably because of the presence of salt glands in the former species. The movement of metals from belowground to aboveground tissues and their release from leaf tissue may be important steps in metal flux in marsh ecosystems. Although metals remaining in the roots are generally considered “out of trouble” as far as release to the environment is concerned, studies are needed regarding the turnover of nutritive roots and the potential release of metals from decomposing roots. Decomposing litter of both species becomes highly enriched in metals over time, and there is evidence that these metals are probably available to detritus feeders. The net influence of this shift in plant species is difficult to determine based on these studies

alone, but they suggest that *S. alterniflora* increases the pool of bioavailable metals and that the invasion of *P. australis* may reduce that pool and play a role in containing metals within contaminated marshes.

Restoration or mitigation plans for contaminated estuaries have not generally included decontamination of sediments as a component of restoration goals. Decisions related to the extensive spread of *Phragmites* in brackish marsh systems in the northeastern US generally involve removing it and replacing it with *Spartina*. Wetland managers concerned with the retention of metals in marsh sediments should consider the benefits of *P. australis* in sequestering metals (as well as nitrogen (Windham, 1999) and greenhouse gases (Brix et al., 2001)) before automatically pursuing traditional restoration efforts that actively remove *P. australis* to restore *S. alterniflora*.

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