Botanical Studies (2007) 48: 453-458.

Invasive and non-invasive plants differ in response to soil heavy metal lead contamination

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(Received September 27, 2006; Accepted May 23, 2007)

ABSTRACT. A greenhouse experiment was conducted to test whether and how invasive species (*Solidago canadensis*) and two non–invasive plant species (*Festuca arundinacea*, *Kummerowia striata*) differed in response to soil heavy metal lead pollution in a mesocosm system. Metal lead was applied as $Pb(AC)_2{\cdot}3H_2O$ in solution at three levels (0, 300 mg kg^{-1} and 600 mg kg^{-1} soil) to simulate a control site and two polluted sites where *S. canadensis* grows. Shoot biomass and N and P uptake of the indigenous species *K. striata* decreased, but those of the introduced species *F. arundinacea* and the exotic invasive species *S. canadensis* increased in Pb polluted soils. Mycorrhizae colonization of the three species and the nodule biomass of *K. striata* were reduced by elevated soil Pb concentration compared to control. Root Pb concentration in invasive *S. canadensis* only accounted for 6.42%, 5.93% and 11.21% of those in non-invasive *K. striata* under corresponding Pb treatments. The results suggested that rapid growth of *S. canadensis* in Pb polluted soil might be due to its ability to exclude Pb or reduce the uptake of Pb compared to non-invasive species.

Keywords: Invasive plant species; Metal lead; Mycorrhizae; N and P uptake.

INTRODUCTION

Solidago canadensis L. (goldenrod), which was introduced from North America into China in the 20th century, has become one of the most destructive invasive weeds in south-eastern China. *Solidago canadensis* was shown to be a superior competitor by producing highly fertile seeds and propagules in its adopted land (Guo and Fang, 2003). Experiments have shown that *S. canadensis* significantly differed from the local species in response to soil N and P, light, temperature, and water availability (Ruan et al., 2004; Guo, 2005; Huang and Guo, 2005a; Lu et al., 2005). For example, Dong et al. (2006) reported that *S. canadensis* was well adapted to low pH soil and tolerant to shading, drought, and low levels of nutrients. It was also found to have colonized well in heavy metal polluted areas. However, whether soil heavy metals interact with the growth and spread of *S. canadensis* is less well known.

Plant species have shown a great many strategies in response to heavy metal (Gerard et al., 2000; Kochian et al., 2002). Experiments reveal that many species have developed a variety of mechanisms to accumulate metals (Cu, As and Zn etc.) and to resist metal stress (Kochian et al., 2002; Yang et al., 2005). Rigola et al. (2006) reported that *Thlaspi caerulescens* has specific genes related to zinc (Zn), cadmium (Cd), and nickel (Ni) accumulation. Sun et al. (2005) found that glutathione (GSH) may be involved in Zn and Pb transport, hyperaccumulation/accumulation and tolerance in mine population of *Sedum alfredii*. Basic et al. (2006) showed that Cd accumulator *Thlaspi caerulescens* with high Cd hyperaccumulation capacity had better growth by developing more and bigger leaves, taller stems, and producing more fruits and heavier seeds. Escaping from heavy metal toxicity by reducing or excluding the uptake of heavy metals may be another strategy for plants to resist metal toxicity. For example, Wei et al. (2005) found that *Oenothera biennis* and *Commelina communis* were Cd-excluders and *Taraxacum mongolicum* was a Zn-excluder. *Oenothera biennis* is a potential Cd-excluder, but also a potential Cu-excluder, implying that these weed species survived well in heavy metal polluted soil by avoiding the uptake of metals.

Symbiotic mycorrhizae are also believed to be a strategy of plant response to heavy metal stress (van Tichelen et al., 2001). Diaz et al. (1996) found that *Glomus mosseae* reduced Zn and Pb accumulation of maize (*Zea mays*) at higher Zn and Pb treatments. Blaudez et al. (2000) also found that under Cu, Cd, Ni, Pb and Zn exposure, mycorrhizae enhanced the efficiency of the N acquisition of birch (*Betula pendula*) seedlings and thereby assisted plants against this metal stress. Mycorrhizal

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fungal structures such as vesicular and hyphae may act as biological barriers that reduce metal Cd translocation from root to shoot of *Trifolium subterraneum* (Joner et al., 2000; Tonin et al., 2001), thus decreasing plant internal sequestration and the negative effects on plant shoot growth.

The main hypotheses for exotic plant invasion that have been proposed are biotic resistance (Maron and Vilá, 2001), superior competitor (Bakker and Wilson, 2001), enemy release (Keane and Crawley, 2002), and allelopathic advantage over resident species (Callaway and Aschehoug, 2000; Bais et al., 2003; Callaway and Ridenour, 2004). However, many invasive plants have shown higher abilities to use water and nutrients under environmental stress (Blicker et al., 2002, 2003). This means that the adaptation or tolerance to stressful environments (water and nutrient limitation, soil pollution) may be an important trait of the exotic invasive plant species.

Therefore, we hypothesize that 1) invasive *S. canadensis* populations grow faster than native species under metal lead polluted soil by excluding Pb or reducing Pb accumulation, and 2) the development of mycorrhizae that coexisted with different plants varies in response to heavy metal. Our objectives were to determine (1) the differences of growth and nitrogen and phosphorus uptake between invasive *S. canadensis* and non-invasive species; (2) the difference of Pb accumulation between invasive *S. canadensis* and non-invasive species.

MATERIALS AND METHODS

Soil and plant species

The soil was collected from a citrus orchard situated at 28°54’ N, 118°30’ E, in the southwestern portion of Zhejiang Province, southeastern China. It was a clayey red soil, equivalent to *Ultisols* in US soil taxonomy, with 70.50% clay, 10.63% silt, 18.79% sand, and pH 4.59 (determined in KCl). The soil had 34.39 g kg^{-1} organic matter, 1.30 g kg^{-1} total N, and 0.95 g kg^{-1} total P. It had 48.08 mg kg^{-1} extractable N, 59.50 mg kg^{-1} extractable P, and 208.23 mg kg^{-1} extractable K. Pb concentration in the soil was 23.27 mg kg^{-1}.

Plant species used in this experiment were *Festuca arundinacea* Schreb., *Kummerowia striata* Thumb. and *Solidago canadensis*. *Festuca arundinacea* is an introduced species that is often used as a cover plant for lawns, roadsides, and green belts next to freeways. *Solidago canadensis* is an invasive species in southern and eastern China (Li et al., 2001; Guo and Fang, 2003). *Kummerowia striata* is an indigenous species usually coexisting with *F. arundinacea* and *S. canadensis* in the field.

Seeds of *F. arundinacea* were obtained from Zhejiang Garden Development Co., LTD (Hangzhou, China) and seeds of *K. striata* were from natural populations in the field. For *S. canadensis*, propagules were used in the experiment since most of its seedlings in the field are generated from propagules (rhizome) and not from seeds (Huang and Guo, 2005b).

Experimental design

The experiment was a randomized complete block design with three Pb levels and four replicates. Three levels of Pb concentration (i.e. ambient, 300 mg kg^{-1} and 600 mg kg^{-1}) were setup to simulate control and two pollution sites where *S. canadensis* grows. Mesocosms (47.5 cm × 34.5 cm × 15.4 cm) were used in this experiment, and each mesocosm was filled with 16 kg soil. Pb was added in the form of $Pb(AC)_2 \cdot 3H_2O$ aqueous solution, and two weeks later soil samples were collected randomly to determine Pb concentrations using the atomic absorption spectroscopy (AAS) method (Lu, 2000). The actual Pb concentrations of the 300 mg kg^{-1} and 600 mg kg^{-1} Pb treatments were 373.93 mg kg^{-1} and 623.57 mg kg^{-1}, respectively.

Seeds and propagules were surface sterilized with 3% NaClO before being sown in the soil. Plant total density was thinned to 30 after seedlings emerged, and each species density remained equal. Mesocosms were arranged in the greenhouse randomly. The plants were maintained in natural light and temperature conditions and were watered daily.

Sampling

The plants were harvested 6 months after seeding. The root nodule of *K. striata* was collected from root and soil. Plant roots were washed with tap water and separated from shoot. Half of the separated root samples were fixed in FAA (37% Formaldehyde-Glacial Acetic Acid-50% Ethanol, 9: 0.5: 0.5, V: V: V) for quantification of AM fungal colonization. The remaining root samples, root nodules, and shoots were oven-dried (80°C for 48 h) and weighed.

Measurements

Root samples were stained with acid fuchsin in lactoglycerol (modified from Koske and Gemma, 1989), and mycorrhizal colonization was quantified from 200 root fragments using the gridline intersect method (Giovannetti and Mosse, 1980) under a stereomicroscope at 40× magnification.

The oven-dried samples of root and shoot were milled with a stainless steel micronizing miller. The fine-ground samples were dried to ash at 600°C for 2 h and then dissolved in 1:1 nitric acid (Lu, 2000). Pb concentrations in the solutions extracted from plant materials (recovery rate 99.5%) were analyzed by the AAS method using a Shimadzu Model AA-6650 atomic absorption spectrometer.

Above and belowground P concentrations of plant sample were measured spectrophotometrically (Murphy and Riley, 1962). Plant N concentration was analyzed by Kjeldahl procedures (2200 Kjeldahl Auto Distillation).

Statistical analysis

Mycorrhizal colonization was arcsine transformed. Normality and homoscedasticity test were performed prior to any treatment, and then the data were submitted to one-way ANOVA or nonparametric analysis with SAS 8.0 for Windows software (v. 8.02, SAS Institute, Cary, NC, USA). LSD was performed for multiple comparisons of means derived from each treatment at a significant level of 0.05.

RESULTS

Plant and nodule biomass

Both aboveground (shoot) and belowground (root and rhizome) biomass of invasive and non-invasive species differed in response to Pb contamination. Compared to control, the biomass of *S. canadensis* increased, but that of *K. striata* decreased under both levels of Pb soil contamination (Figure 1). For *F. arundinacea*, shoot biomass increased under 300 mg kg^{-1} but decreased under 600 mg kg^{-1}. In addition, the nodule biomass of *K. striata* fell by 34.38% and 59.38%, respectively, under the 300 mg kg^{-1} and 600 mg kg^{-1} treatments compared to control.

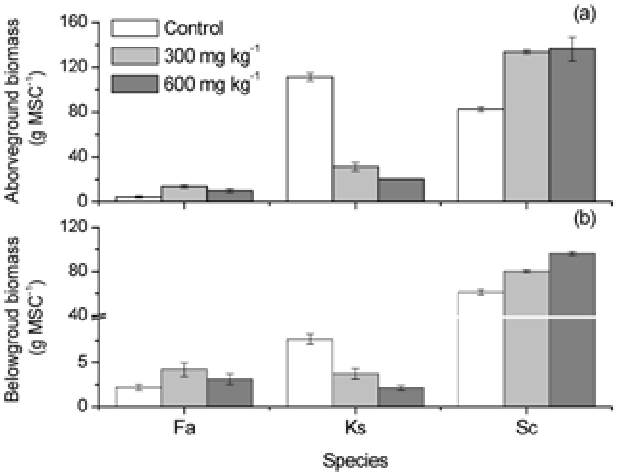

Figure 1. Aboveground (shoot) and belowground (root and rhizome) biomass (g·MSC^{-1}) of three species as affected by Pb treatments. Fa, *Festuca arundinacea*; Ks, *Kummerowia striata*; Sc, *Solidago canadensis*; MSC, mesocosm. Error bars represent SE.

Mycorrhizal colonization

Mycorrhizal colonization of the three species fell under Pb contamination, but the magnitude of reduction for *S. canadensis* was significantly higher than for *F. arundinacea* or *K. striata* (Figure 2). Compared to control, colonization of *S. canadensis* and *F. arundinacea* decreased in both the 300 mg kg^{-1} and 600 mg kg^{-1} Pb treatments, but the colonization of *K. striata* did not change at 300 mg kg^{-1}.

Shoot N and P contents

Shoot N and P contents of *F. arundinacea* and *S. canadensis* increased under both the 300 mg kg^{-1} and 600 mg kg^{-1} Pb treatments while those of *K. striata* decreased compared to control (Figures 3 and 4).

Shoot and root Pb concentration

No significant difference of shoot Pb concentration was found among the three species under either control or the 300 mg kg^{-1} and 600 mg kg^{-1} Pb treatments (Figure 5a). Compared to control, Pb treatments significantly enhanced Pb concentration in roots of all three species. However, Pb concentration was significantly lower in roots of *S. canadensis* than in *F. arundinacea* and *K. striata* under both control and Pb treatments (Figure 5b).

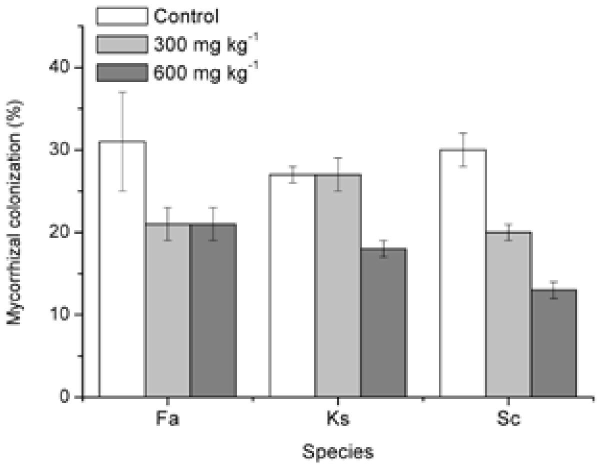

Figure 2. Mycorrhizal colonization of three species under control and Pb treatments. Fa, *Festuca arundinacea*; Ks, *Kummerowia striata*; Sc, *Solidago canadensis*; Error bars represent SE.

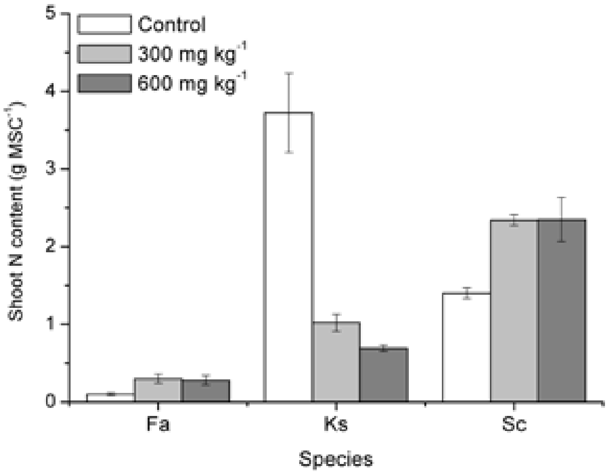

Figure 3. Shoot N content of three species under control and Pb treatments. Fa, *Festuca arundinacea*; Ks, *Kummerowia striata*; Sc, *Solidago canadensis*; MSC, mesocosm. Error bars represent SE.

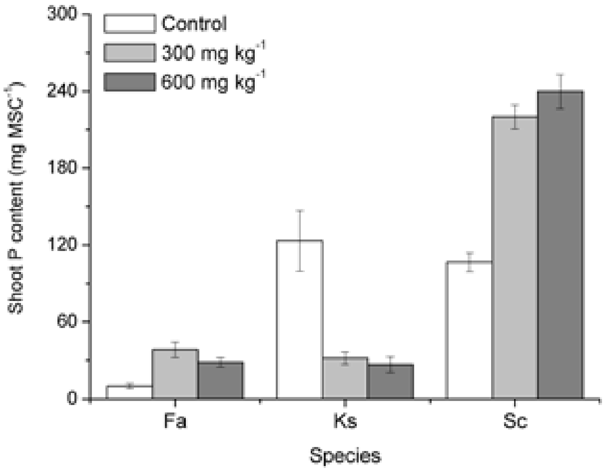

Figure 4. Shoot P content of three species under control and Pb treatments. Fa, *Festuca arundinacea*; Ks, *Kummerowia striata*; Sc, *Solidago canadensis*; MSC, mesocosm. Error bars represent SE.

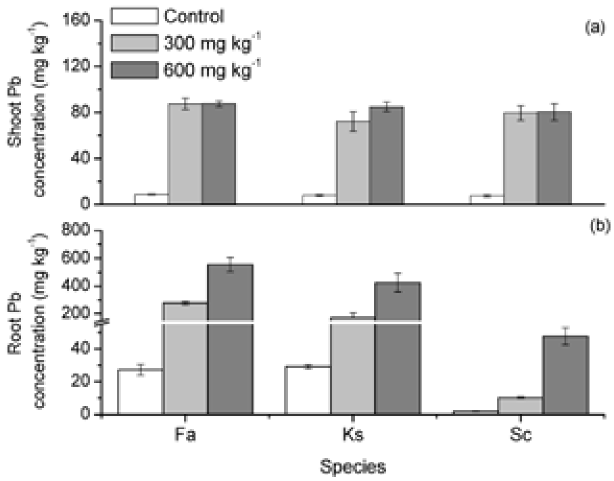

Figure 5. Shoot (a) and root (b) Pb concentration of three species under control and Pb treatments. Fa, *Festuca arundinacea*; Ks, *Kummerowia striata*; Sc, *Solidago canadensis*; Error bars represent SE.

DISCUSSION

Invasive plant species are often characterized by their abilities to transcend stress conditions that constrain native species and to compete for limited resources to obtain rapid growth (Uveges et al., 2002; Seabloom et al., 2003; Kercher and Zedler, 2004). This was reflected in our experiment. Although Pb concentrations in plant roots consistently increased with soil Pb concentration, the magnitude differed from plant to plant. For *S. canadensis,* root Pb concentrations were much lower, accounting for only 6.42%, 5.93% and 11.21% of those in the roots of *K. striata* under corresponding Pb treatments (Figure 5). It is well known that excessive heavy metal can adversely affect plant growth, development, and reproduction (Monni et al., 2001; Brun et al., 2003; Kim et al., 2003; Ryser and Sauder, 2006). Therefore, the advantages resulting from low Pb accumulation could be dramatic in the competition with resident species. How *S. canadensis* reduces its Pb uptake is still unknown. Our results showed that *K. striata* acquired higher N and P contents under ambient soil than *F. arundinacea* and *S. canadensis* while its N and P contents were far lower than those of *S. canadensis* under elevated soil Pb (Figures 3 and 4). This evidence might be partially due to the high Pb concentration accumulated in the root of *K. striata* since heavy metals may inhibit its uptake of nutrients from the soil (Blaudez et al., 2000). Soil nutrient availability has a profound effect on the invasibility of a plant community according to the fluctuating resources availability theory (Davis et al., 2000; Davis and Pelsor, 2001; Burns, 2004). The theory deems that a plant community becomes more susceptible to invasion after an increase in the amount of unused resources. Heavy metal tended to negatively affect nutrient mineralization, and this in turn affected nutrient availability (Vásquez-Murrieta et al., 2006). However, the nutrients (N and P) used by *K. striata* also declined significantly under Pb treatments, and therefore the amount of unused nutrients in the soil might have increased. Thus, *S. canadensis* might utilize N and P more efficiently and would undoubtedly dominate the community under elevated Pb soil. As with nutrient uptake, the shoot biomass of *K. striata* decreased but that of *F. arundinacea* and *S. canadensis* increased when exposed to elevated Pb soils (Figure 1). In addition, root nodule biomass of *K. striata* fell by 34.38% and 59.38%, respectively, under the 300 mg kg^{-1} and 600 mg kg^{-1} Pb treatments. The loss of symbionts would inevitably have further influence on nitrogen fixation. A causal relationship between Pb accumulation, nutrient uptake, and plant growth is very likely. *Solidago canadensis* gained no advantage over, and was even inferior to, *K. striata* in terms of growth and nutrient uptake under ambient soil, but it became a superior competitor under elevated Pb soils. In other words, ecophysiological traits and invaded soil properties facilitated the invasion of *S. canadensis*. This implies that Pb-polluted soil may be more vulnerable to invasion by *S. canadensis*.

Mycorrhizae were shown to protect host plants against metal toxicity by enhancing P uptake (van Tichelen et al., 2001; Chen et al., 2005), but in our experiment, mycorrhizal colonization decreased in all three plant species under elevated Pb treatments, and the magnitude of the mycorrhizal colonization decrease was higher in *S. canadensis* than in *K. striata* and *F. arundinacea* (Figure 2). Mycorrhizal colonization did not correlate with the nutrient uptake or Pb exclusion of *S. canadensis,* and this did not support our hypothesis.

In conclusion, the invasive species *S. canadensis* and non-invasive species *K. striata* and *F. arundinacea* differed in response to soil Pb pollution. Although no significant difference of shoot Pb concentration was evident among the three species, Pb concentrations in roots of *K. striata* were much higher than in the roots of *S. canadensis*. Mycorrhizae of all these species were inhibited by higher Pb concentration in soils. The above and belowground biomass and the N and P uptake of *S. canadensis* increased but those of *K. striata* decreased under elevated Pb soils. This suggests that rapid growth of *S. canadensis* in Pb polluted soil might be due to its ability to exclude Pb or reduce the uptake of Pb.

Acknowledgements. This study was supported by the Natural Science Foundation of Zhejiang Province (NSFZJ No. R 505024) and the National Natural Science Foundation of China (NSFC, No.39870149, 30228005, and 30030030).

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入侵植物和非入侵植物對土壤重金屬鉛污染的不同響應

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通過在溫室內進行的中宇宙試驗檢驗了入侵植物（加拿大一枝黃花）和兩種非入侵植物（高羊茅、雞眼草）對土壤重金屬鉛污染的響應是否以及如何存在差異。本研究通過在土壤中加入三個水平的醋酸鉛溶液來模擬對照土壤以及有加拿大一枝黃花生長的兩種重金屬污染的土壤。本地種雞眼草的地上部分生物量、N 和 P 的吸收量在鉛污染土壤中顯著下降；而引入種高羊茅以及入侵種加拿大一枝黃花在鉛污染土壤中則顯著提高。與對照相比，鉛污染顯著降低了雞眼草的菌根侵染率和根瘤生物量。入侵種加拿大一枝黃花的根部鉛濃度分別為雞眼草各個鉛處理中根部鉛濃度的 6.42%，5.93% 和 11.21%。結果表明，鉛污染土壤中加拿大一枝黃花的快速生長是由於與非入侵種相比它具有減少或排斥鉛吸收的能力。

關鍵詞：入侵植物；重金屬鉛；菌根；N 和 P 吸收。