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Competitive interaction between the invasive *Solidago canadensis* and native *Kummerowia striata* in lead contaminated soil

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ABSTRACT. Higher tolerance to stressful environments may result in exotic plants being more competitive than native ones, thus promoting plant invasion. We conducted a greenhouse experiment to test this hypothesis by using invasive *Solidago canadensis* and native *Kummerowia striata* as model plant species under lead contamination. 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 control and two pollution sites on which *S. canadensis* was found. Invasive *Solidago canadensis*, native *Kummerowia striata*, and their combination were grown under each Pb treatment. Under monoculture no differences of biomass, nitrogen (N) or phosphorus (P) contents in *S. canadensis* were found among treatments, but the growth of native *K. striata* was significantly depressed at higher soil Pb concentration. When both species were mixed, elevated soil Pb concentrations significantly increased shoot biomass ratio of *S. canadensis* to *K. striata*, implying that Pb enhanced the competition of *S. canadensis* over *K. striata*. Compared to monoculture, biomass and N and P contents of *S. canadensis* significantly increased under mixture with *K. striata* in each Pb treatment. Under both monoculture and mixed culture, Pb concentrations in shoots, roots, and rhizomes of *S. canadensis* increased with soil Pb content, but Pb concentrations in both above- and below-ground tissues of *S. canadensis* were significantly lower in mixture than that in monoculture under each Pb treatment. Both Pb treatments and mixture with native *K. striata* did not change biomass allocation to shoot, root and rhizome of *S. canadensis*. Evidence from our experiment supported the hypothesis that higher tolerance to Pb stress enabled the invasive *S. canadensis* to outperform the native *K. striata* and may have promoted its rapid invasion in Pb contaminated soil.

Keywords: Heavy metal contaminated soil; Invasive *Solidago canadensis*; Native *Kummerowia striata*; Monoculture; Mixture.

INTRODUCTION

The competitive performance of invasive species is often habitat-dependent (Daehler, 2003). Some invasive species possess higher tolerance to environmental stress (e.g., excess cations, salinity, low temperature and pollution), which can drive the species invasion into new ranges (Uveges et al., 2002; Kercher and Zedler, 2004; Funk and Vitousek, 2007). Experiments have shown that tolerance to drought (Cleverly et al., 1997), flood (Newman et al., 1996), turbidity (Thomsen and McGlathery, 2007), and low resources (Funk and Vitousek, 2007) allowed some invasive species to outperform natives in a stressful environment.

An exotic plant species' ability to be highly competitive is widely recognized as an important attribute in plant invasion (Bakker and Wilson, 2001; Levine et al., 2003; Vilá and Weiner, 2004; Minchinton et al., 2006). When an exotic species is introduced, competition for limited resources is probably the first interaction that the species has with native species in the recipient community. Studies have shown that the magnitude and outcome of such interactions may shift due to disturbance or other habitat modifications (Petren and Case, 1998; D'Antonio et al., 1999), resources and fluctuations in their availability (Davis et al., 2000; Davis and Pelsor, 2001), stressful conditions (Claassen and Marler, 1998; Daehler, 2003), and adaptation of the exotic species to its new habitat in relation to its multiple introductions (Besnard et al., 2007; Broennimann et al., 2007; Facon et al., 2008). Thus linking biotic interactions such as competition to environmental changes may be critical to our understanding of how and why an exotic plant species is likely to invade successfully or expand its range.

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In the present study, we examined whether and how soil lead pollution affects the outcome of competitive interaction between exotic and native species, and we used the invasive *Solidago canadensis* and native *Kummerowia striata* as model species. *Solidago canadensis* L. (goldenrod), one of the most destructive invasive weeds in southeastern China, was introduced from North America. *Solidago canadensis* adapted well to low pH and was tolerant to shading, drought, and nutrient deficiency (Dong et al., 2006; Song et al., 2007). Its response to soil N and P, light, temperature, and soil water differed from that of local species (Guo and Fang, 2003; Ruan et al., 2004; Guo, 2005; Huang and Guo, 2005; Lu et al., 2005). Our preliminary studies also showed that *S. canadensis* was highly tolerant to Pb and could easily colonize and establish itself in heavy metal polluted areas (Yang et al., 2007), but whether heavy metal could alter the interaction of *S. canadensis* with native species remains a question. *Kummerowia striata* Thumb. is a Chinese native and common weedy species in many crop fields and natural habitats (Chen et al., 2004, 2005). *Kummerowia striata* also commonly coexists with *S. canadensis* in lands invaded by the latter (Yang et al., 2007). Understanding the effects of soil pollution stress on the interaction of invasive and native plants will provide insights into the invasion mechanisms of *S. canadensis* and possibly also into potential methods of controlling this species.

MATERIALS AND METHODS

Soil and plant species

The soil for experiments was collected from a citrus orchard situated at 28°54’ N, 118°30’ E in southwestern Zhejiang Province, southeastern China. It was a clayey red soil, equivalent to *Ultisols* in US soil taxonomy, with a pH of 4.59 (determined in $CaCl_2$). The soil had 34.4 g kg^{-1} organic matter, 28.1 mg kg^{-1} extractable N, 8.99 mg kg^{-1} extractable P, and 108.2 mg kg^{-1} extractable K. Total lead concentration in the soil was 23.3 mg kg^{-1}.

Seeds of *K. striata* and propagules (un-germinated buds) of *S. canadensis* were collected from their natural populations in a field in Hangzhou city, Zhejiang Province.

Experimental design

The experiment was a two-factorial design with different Pb levels and culture types. Three levels of Pb (0, 300 and 600 mg kg^{-1} soil) were used to simulate uncontaminated soil and two levels of Pb pollution at sites where *S. canadensis* was spreading. Culture types included two monocultures of each plant species (invasive *S. canadensis* and native *K. striata*) and a combination of the two species at an equal plant number (1:1). There were four replicates for each treatment.

Mesocosms (47.5 cm × 34.5 cm × 15.4 cm) were used in this experiment, and each was filled with 16 kg soil. Pb was applied as lead acetate ($Pb(CH_3COO)_2{\cdot}3H_2O$). Seeds and propagules were surface sterilized with 3% NaClO before being sown in the soil. Twelve propagules of *S. canadensis*, 12 seeds of *K. striata* and their mixture (6 propagules and 6 seeds, respectively) were planted in each mesocosm, and these were arranged in a greenhouse in a completely randomized block design. Plants were maintained under natural light and temperature conditions. Natural air temperature varied from 18 to 30°C during the experiment from April to October. Plants were watered daily to keep soil moisture at 70-90% of water-holding capacity. No additional nutrients were given during the experiment.

Sampling and measurements

Plants were harvested 120 days after seeding. Plant roots were washed with tap water to remove soil particles and separated from shoots. For *S. canadensis*, rhizome was separated from root and shoot. Plant samples were oven-dried (80°C for 48 h) and weighed. The oven-dried samples were milled with a stainless steel micronizing miller. Above- and below-ground plant tissues were analyzed for their N concentrations by Kjeldahl procedures (2200 Kjeldahl Auto Distillation). Plant P concentrations were measured by spectrophotometry (UV-1600 spectrophotometer, Beijing, Murphy and Riley, 1962). The fine-ground plant samples were dried to ash at 600°C for 2 h and then dissolved in 1:1 nitric acid (Bao, 2000). Concentrations of Pb in the solutions extracted from plant materials (recovery rate 99.5%) were analyzed by the AAS (Atomic Absorption Spectrometry) method using an atomic absorption spectrometer (Shimadzu Model AA-6650).

Statistical analysis

Two-way ANOVA was done for each dependent variable using the general linear model (GLM) design in the SPSS V.10.0 (SPSS Inc., Chicago). The independent variables were Pb concentrations and types of plant culture (monoculture or mixture). Least significant difference (LSD) at the 5% confidence level was used for comparison between treatments.

RESULTS

Biomass

The total biomass of invasive *S. canadensis* under both monoculture and mixed culture with *K. striata* was not affected by Pb treatments ($P>0.05$) (Figure 1), but elevated Pb concentration significantly reduced total biomass of native *K. striata* ($P<0.05$). Biomass allocation to shoots, roots and rhizomes of *S. canadensis* was not significantly affected by Pb treatments under either culture condition ($P>0.05$) (Figure 2a). Compared with the control, elevated Pb treatments significantly reduced ($P<0.05$) biomass allocation to roots in *K. striata* (Figure 2b), but no difference ($P>0.05$) in biomass allocation was found between monoculture and mixed culture under any Pb treatment (Figure 2b). In cohabitation, the shoot biomass ratio of *S. canadensis* to *K. striata* significantly increased ($P<0.05$)

with the soil Pb concentration (Figure 3).

N and P contents in plants of *S. canadensis*

Pb treatments significantly increased (P>0.05) the total N content in plants of *S. canadensis* under mixed culture but not in monoculture (Figure 4a). P content in *S. canadensis* was significantly higher (P<0.05) in elevated Pb treatments than in control in both monoculture and mixture (Figure 4b). No difference in total P content was found between monoculture and mixture under elevated Pb treatments (Figure 2b), but under control, P content was significantly higher (P<0.05) in monoculture than in mixture (Figure 4b).

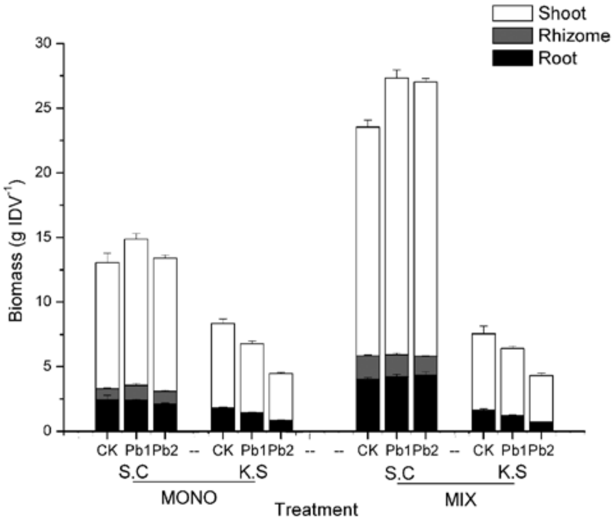

Figure 1. Shoot, root and rhizome biomass of *S. canadensis* and shoot and root biomass of *K. striata* as affected by soil Pb treatments under monoculture and mixture. CK means no Pb addition treatment; Pb1 means 300 mg kg^{-1} treatment; Pb2 means 600 mg kg^{-1} treatment. S.C means *S. canadensis*; K.S means *K. striata*. MONO means monoculture; MIX means mixture. IDV means individual plant. Values are means ± S.E.

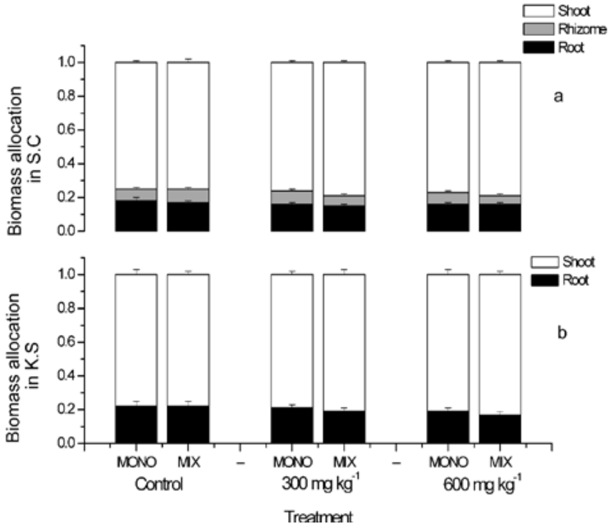

Figure 2. Biomass allocation of *S. canadensis* and *K. striata*. MONO means monoculture; MIX means mixture. S.C means *S. canadensis*; K.S means *K. striata*. Values are means ± S.E.

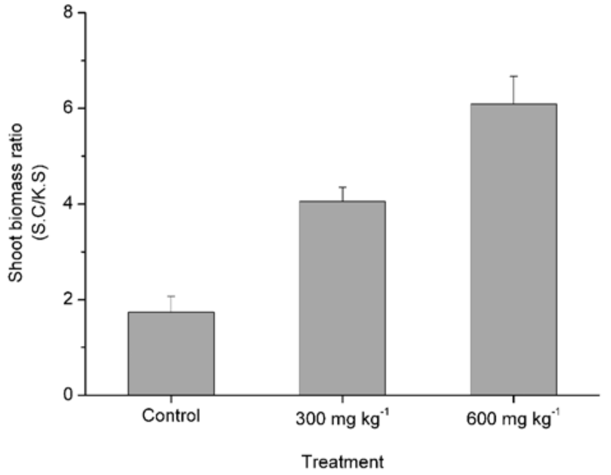

Figure 3. Total shoot biomass ratio of *S. canadensis* to *K. striata* in a mesocosm under mixture. S.C means *S. canadensis*; K.S means *K. striata*. Values are means ± S.E.

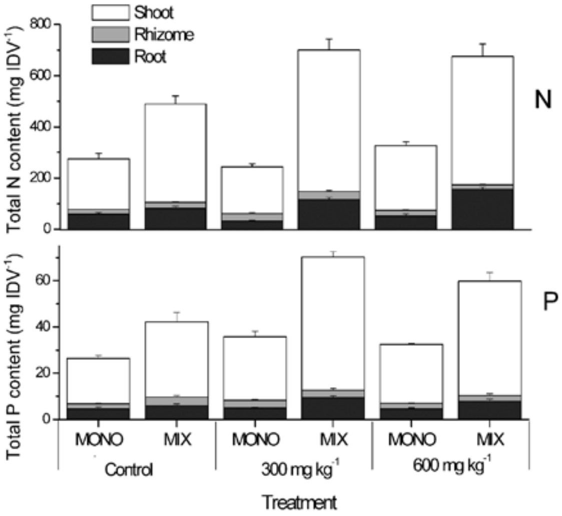

Figure 4. Nitrogen (N) and phosphorous (P) content in shoot, root, and rhizome of individual plant of *S. canadensis* plant as affected by soil Pb treatments under monoculture and mixture. MONO means monoculture; MIX means mixture. IDV means individual plant. Values are means ± S.E.

Pb concentration in shoots and roots

Shoot and root Pb concentrations in native *K. striata* were significantly higher (P<0.05) than those in the invasive *S. canadensis*, regardless of Pb treatment and culture mode (Figures 5 and 6). Elevated soil Pb levels significantly increased (P<0.05) Pb concentrations of the above- and below-ground parts in both *S. canadensis* and *K. striata* (Figures 5 and 6). Shoot, root and rhizome Pb concentrations of *S. canadensis* in mixed culture were lower ($P<0.05$) than those under monoculture (Figure 5), but the reverse was true for the shoot and root Pb concentrations in *K. striata* (Figure 6).

DISCUSSION

Solidago canadensis is a successful invader with a high tolerance to shading, drought, nutrient depletion, and Pb contamination (Dong et al., 2006; Yang et al., 2007). Higher soil Pb did not affect its growth, but it greatly reduced native plants under monoculture (Yang et al., 2007). When grown in the presence of native *K striata*, Pb treatments enhanced the success of *S. canadensis* over *K striata* in our experiments. The shoot biomass ratio of *S. canandensis* to *K striata* was 1.8 in the control without Pb addition, but under higher soil Pb concentrations the ratio increased to 4.1 (300 mg kg^{-1} treatment) and 6.1 (600 mg kg^{-1} treatment). This suggested that *S. canadensis* gained less advantage over *K. striata* in terms of biomass in normal soil while under elevated Pb soils, it became a superior competitor. Plant species with higher competitive ability often possesses a greater capacity to acquire resources (Thorsted et al., 2006), an ability to more rapidly occupy space (Williams, 1963; Sekimura et al., 2000), and a higher tolerance to disturbances or environmental stress (del-Val and Crawley, 2004; Rogers and Siemann, 2004). The higher competitiveness of *S. canadensis* is probably attributable to its higher tolerance to soil Pb than *K. striata* (Yang et al., 2007), thus higher soil Pb levels could be a crucial selective factor that enhances the growth of *S. canandensis* and drives the outcome of the competitive interaction in the metal contaminated soil.

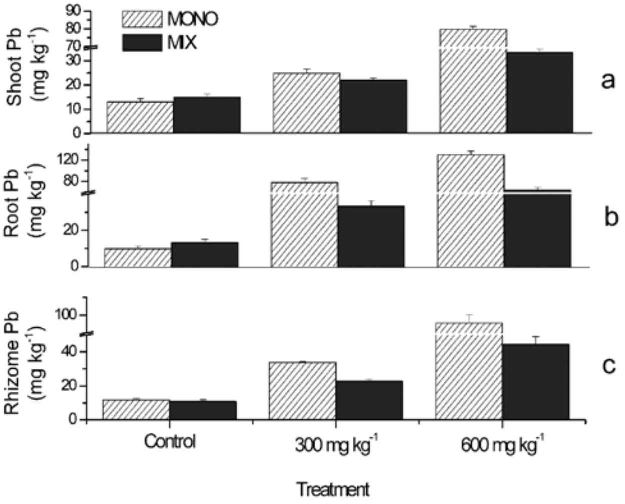

Figure 5. Lead concentration in shoot (a), root (b), and rhizome (c) of *S. canadensis* as affected by soil Pb treatments under monoculture and mixture. MONO means monoculture; MIX means mixture. Values are means ± S.E.

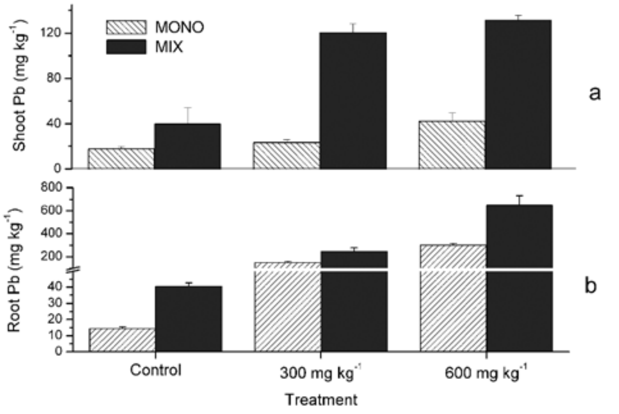

Figure 6. Lead concentration in shoot (a) and root (b) of *K. striata* as affected by soil Pb treatments under monoculture and mixture. MONO means monoculture; MIX means mixture. Values are means ± S.E.

One of the strategies for tolerance to metal toxicity is that plants avoid accumulation of heavy metals through exclusion or reducing uptake (Wei et al., 2005). In our experiments, *S. canadensis* outperforming *K. striata* in higher Pb soil concentrations could be probably explained by differential Pb accumulation in exotic and native plant species under monoculture and mixture. Pb concentrations in the shoots, roots, and rhizomes of *S. canadensis* were significantly lower under mixture than monoculture (Figure 5), and this disparity was particularly obvious under higher Pb treatment (600 mg kg^{-1}). However, for native *K. striata*, shoot and root Pb concentrations were higher under mixture than under monoculture, particularly in the 300 and 600 mg kg^{-1} treatments (Figure 6). *Solidago canadensis* reduced or excluded Pb uptake, which resulted in a higher Pb concentration in rhizospheric soil. This may have enhanced the Pb uptake and accumulation by the neighboring *K. striata* in the mixture. The enhanced Pb accumulation would have inhibited the growth and nutrient (N and P) uptake of *K. striata*; resulting in an increase in resources (space and nutrients) for *S. canadensis*. These alterations of the rhizosphere environment may have partially contributed to the increase in biomass and N and P contents in *S. canadensis* under coinhabitation. One alternative explanation is that *S. canadensis* altered the rhizospheric soil environment through reducing and excluding Pb uptake in polluted soil, which had a negative impact on *K. striata* and in turn favored itself.

Differences in phenotypic plasticity in characters (e.g., photosynthetic rate, shoot height, leaf number and area, and biomass allocation to shoot and root) between invasive and native species may also attribute to the aggressiveness of exotic species (Schweitzer and Larson, 1999; Kaufman and Smouse, 2001) although different results were found in other experiments (Williams and Black, 1994; DeWalt et al., 2004). Biomass allocation to functionally distinct tissues was thought to be important in enhancing access to a specific resource in shoot supply (Sultan, 2003). In our experiments, we examined the biomass allocation of

S. canadensis under Pb contaminated conditions, with or without the native plant. Biomass allocation to shoots, roots, and rhizomes did not significantly change after the addition of Pb or in the presence of *K. striata,* suggesting that plasticity in biomass allocation was not an important driving factor in *Solidago's* adaptation to Pb contamination.

In conclusion, our results indicated that the invasive *S. canadensis* had higher Pb tolerance than the native *K. striata*, probably because the former reduced its Pb uptake. Elevated soil Pb concentrations enhanced the growth of *S. canadensis* over *K. striata* in mixture. Neither soil Pb nor the presence of *K. striata* changed the biomass allocation to shoots, roots, and rhizomes of *S. canadensis*. These results supported the hypothesis that Pb contamination affects the interaction between *S. canadensis* and *K. striata*, attributable to the greater tolerance of *S. canadensis* to Pb stress.

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重金屬鉛污染條件下入侵植物加拿大一枝黃花和中國原生植物雞眼草的競爭性相互作用

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作者首先提出這樣一個科學假說：對逆境環境具有較強耐性可能造成入侵物種比本地物種具有較強競爭能力，從而促進其入侵過程。本研究借助於溫室試驗，通過入侵物種加拿大一枝黃花和本地物種雞眼草的單作和混植試驗，證驗了這一假說。重金屬鉛以醋酸鉛 [$Pb(AC)_2 \cdot 3H_2O$] 溶液為鉛加入形態，設置 0、300、600 mg/kg 共三個施入濃度，以模擬對照生境和兩個鉛污染土壤生境。每重土壤條件下分別種植入侵物種加拿大一枝黃花和本地物種雞眼草及其組合。結果表明，單作條件下三種鉛處理濃度的加拿大一枝黃花的生物量、氮含量及磷含量沒有顯著差異，但本地物種雞眼草的生長卻隨著土壤鉛濃度的增加發生了顯著的下降。混植條件土壤鉛濃度增加拿大一枝黃花和種雞眼草地上部生物量的比，表明土壤鉛增強加拿大一枝黃花對種雞眼草的競爭。與單作相比，混植條件下加拿大一枝黃花地上部和地下部分的生物量、氮含量、磷含量顯著較高，每種鉛土壤濃度下均表現如此。無論是在單作還是在混植條件下，加拿大一枝黃花的地上部、根狀莖、根系中的鉛含量都隨著土壤鉛濃度的不斷增加而增加；但不同鉛濃度下，混植條件下加拿大一枝黃花地上部和地下部的鉛濃度均顯著低於單作。鉛濃度處理以及與雞眼草混作均不改變加拿大一枝黃花生物量在地上部、根莖及根系中的分配比例。這些證據支持了我們的假說，即加拿大一枝黃花對鉛脅迫的較強耐性使得其在鉛污染土壤中的表現明顯優於本地物種，從而導致了外來入侵物種加拿大一枝黃花在鉛污染土壤的快速入侵。

關鍵詞：重金屬污染土壤；入侵物種加拿大一枝黃花；本地物種雞眼草；單作。