



# Autotoxicity of root exudates varies with species identity and soil phosphorus

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## Abstract

Root exudate autotoxicity (i.e. root exudates from a given plant have toxic effects on itself) has been recognized to be widespread. Here we examined how plant species identity and soil phosphorus (P) availability influenced this autotoxicity and the possible stoichiometric mechanisms. We conducted an experiment with three species (*Lactuca sativa*, *Sesbania cannabina*, and *Solidago canadensis*), which were subject to four treatments consisting of activated carbon (AC) and soil P. AC addition increased the whole-plant biomass of each species under high P conditions and this AC effect varied strongly with species identity. For *Solidago*, the relative increase in whole-plant biomass due to AC addition was larger in the low P than in the high P. Root exudate autotoxicity differed between roots and shoots. AC addition decreased root N:P ratios but failed to influence shoot N:P ratios in three species. These findings suggest that soil P enrichment might mediate root exudate autotoxicity and that this P-mediated autotoxicity might be related to root N and P stoichiometry. These patterns and their implications need to be addressed in the context of plant communities.

## Highlights

- Root exudate autotoxicity varied with species identity and soil P.
- Root exudate autotoxicity differed between roots and shoots.
- P-mediated autotoxicity might be related to N:P ratios.

**Keywords** Competition · Plant species identity · Root exudate autotoxicity · Soil P availability · Stoichiometry

## Introduction

In a general sense, autotoxicity can be defined as the process whereby the presence of a given plant species has toxic effects on the species itself directly or indirectly (Muller 1966; Rice 1974; Wise and Abrahamson 2017). Similarly, root exudate autotoxicity can be defined as the process

whereby root exudates from a specific plant have toxic effects on itself. Overall, root exudate autotoxicity is fundamentally related to two facets: chemicals released from plant roots (i.e. internal pathways), and soil conditions/and their changes (i.e. external pathways) (Muller 1966; Rice 1974; van der Putten et al. 2016). Here, we aimed at root exudate autotoxicity for the following reasons. First, root exudates play a key role in internal pathways. For example, root exudates can affect the metabolite production, photosynthesis, and respiration of plants (Weir et al. 2004), and root allelopathic compounds can delay seed germination and reduce root elongation (Perry et al. 2005). Second, root exudates are present as a whole in the field and complete root exudates dramatically differ from their individual components in ecological functions (Bais et al. 2006). In light of online search at the Web of Science, there have been considerable reports about chemical allelopathy, but relatively limited information is available about the autotoxicity of root exudates.

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Root exudate autotoxicity has long been demonstrated to be quite widespread from ferns through conifers to flowering plants (Rice 1974; Munther and Fairbrothers 1980), but most of the current knowledge about this autotoxicity stems mainly from crop plants primarily because it can cause economically obvious losses by decreasing crop yield and quality (Bu et al. 2016, 2018). In natural plant communities, root exudate autotoxicity does not necessarily mean ecologically detrimental consequences, especially at long-term and/or larger scales. For example, autotoxicity can favor species coexistence and increase species diversity by decreasing competition (Guzmán-Guillén et al. 2017; Wang et al. 2019).

Of all factors determining root exudate autotoxicity, we focused on plant species identity and soil P availability. There are diverse growth forms in plant species, and this diversity can influence plant performance such as growth, development, and reproduction (Crawley 1997; Freschet et al. 2018). Similarly, plants differing in growth forms may exhibit contrasting autotoxicities primarily because they can yield differential root exudates (Rovira 1969; Bais et al. 2006). In the field, P is among the most important soil nutrients limiting ecosystem functioning (Elser et al. 2007). On the other hand, intensive agricultural practices have greatly increased soil P contents over the past decades, which in turn may have complex effects on plants (Hobbs and Huenneke 1992). Soil P availability has a tight connection with root exudates. For example, organic acids in root exudates can increase the availability of soil phosphate (Hinsinger 2001) and P deficiency can affect the composition and production of root exudates (Johnson et al. 1996; Bertin et al. 2003).

The aim of this study was to understand how species identity and soil P influenced root exudate autotoxicity and the possible stoichiometric mechanisms. Accordingly, we proposed the following hypotheses: (1) root exudate autotoxicity might differ among annual, biennial, and perennial plants; (2) root exudate autotoxicity might vary with soil P availability; (3) root exudate autotoxicity might be related to N:P ratios. To test these hypotheses, we conducted an experiment with three plant species grown under four AC and P treatments, and determined whole-plant biomass, root biomass, shoot biomass, root N:P ratios, and shoot N:P ratios.

## Materials and methods

### Experimental design

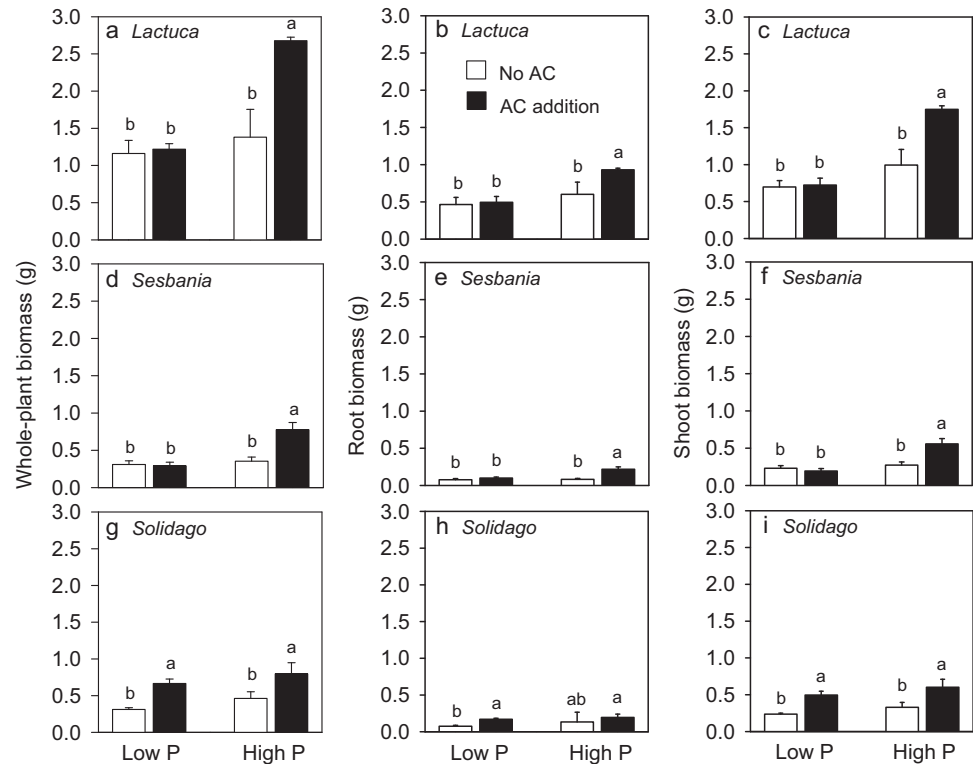
In this experiment, three plant species (*Lactuca sativa* L. [Asteraceae, biennial herb], *Sesbania cannabina* (Retz.) Poir. [Fabaceae, annual herb], and *Solidago canadensis* L.

[Asteraceae, perennial shrub]) were chosen for the following reasons: they have different growth forms and different growth rates, and often occupy different habitats (Editorial Board of Flora of China 1985, 1990). We set up four treatments consisting of AC and P, each with two levels. Each species was subject to one of the four treatments. Accordingly, this experiment included 12 combinations (2 AC treatments  $\times$  2 P levels  $\times$  3 species = 12 combinations).

We used a mixture of 1:1 sand and vermiculite as growth substrate, because this substrate might minimize confounding effects (e.g. soil microbes alone and soil microbe–root exudate interactions), and enabled us to completely harvest roots at the end of the experiment. Experimental plants were grown in growth substrate either with AC or without AC. More specifically, we added 2% of AC (Sinopharm Chemical Reagent Co., Ltd., Shanghai, China) to adsorb root exudates as this dose has been widely used in previous studies (Callaway and Aschehoug 2000; Abhilasha et al. 2008). Similarly, experimental plants were grown in either low or high P conditions. For low P, 50 mL of a 0.20% solution of a water-soluble fertilizer (Peters Professional, Scotts, USA; N–P–K [20–20–20]) were supplied at one-month intervals (20 ppm soil P in total); for high P, 50 mL of a 0.20% solution of a water-soluble fertilizer and 50 mL of a 0.12% solution of P<sub>2</sub>O<sub>5</sub> were supplied at one-month intervals (80 ppm soil P in total). Note that a solution of fertilizer was used in our study, thereby guaranteeing the homogeneity of P application. These two P levels correspond roughly to lower and higher P levels in the field (Wang and Zhang 2004; Xu 2009).

All plants were grown from seed in 1 L pots (top diameter 10 cm, bottom diameter 6 cm, and height 20 cm). Once seeds germinated, we thinned seedlings to only one per species in a pot. In other words, there was only one species in a pot and each species had only one seedling. There were 10 replicates for each species–treatment combination, in total 120 pots. This experiment was conducted in a greenhouse at the Institute of Botany, Chinese Academy of Sciences, where the temperature and humidity were maintained between 20 and 30 °C and 50–60%, and the photosynthetically active radiation during the day remained above 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Over the experiment, all pots were randomly rotated every week to avoid the possible effects of greenhouse microsite variability and all plants were supplied with water at 1–3 day intervals as required to be sure that larger plants did not become relatively more water-limited than smaller plants (i.e. no drought stress). If the same amount of water was supplied, then it was possible that soil water content differed among pots due to non-proportional water losses caused by plants with contrasting sizes. And the other growing conditions were identical for all plants. Our experiment lasted from late May through early September.

**Fig. 1** **a** Whole-plant biomass, **b** root biomass, and **c** shoot biomass of *Lactuca sativa*, **d** whole-plant biomass, **e** root biomass, and **f** shoot biomass of *Sesbania cannabina*, and **g** whole-plant biomass, **h** root biomass, and **i** shoot biomass of *Solidago canadensis* grown under four conditions consisting of activated carbon (AC) and soil P. Data are means  $\pm$  1 SE



At the end of the experiment, all plants were harvested, separated into roots and shoots, rinsed, oven-dried at 80 °C for 48 h, and weighed. The dry plant materials (i.e. roots and shoots) were ground into a fine powder and passed through a 1-mm mesh sieve before N and P analyses. The N content of all the samples was determined using an elemental analyzer (CE 440, EAI, USA), and their P content was determined by extracting with 25 mL mixture of 0.05 M HCl and 0.025 M H<sub>2</sub>SO<sub>4</sub> and analyzing with a UV-visible spectrophotometer (UV-2550, Shimadzu Corporation, Japan).

## Data analyses

The whole-plant biomass was defined as the sum of root dry biomass and shoot dry biomass. Root exudate autotoxicity was evaluated by the difference in whole-plant biomass, root biomass or shoot biomass between plants grown in substrate with AC and plants grown in substrate without AC. The great difference indicates strong autotoxicity. To contrast root exudate autotoxicity among species or parts, we standardized this autotoxicity through calculating the relative change (RC) in biomass as follows:  $RC = (Biomass_{AC\ addition} - Biomass_{no\ AC}) / Biomass_{no\ AC} \times 100\%$ , where Biomass is the whole-plant biomass, root biomass or shoot biomass of a given species. The N:P ratios were expressed as mass ratios (g N/g P). The variables were log-transformed to meet the assumptions of analysis of

variance (ANOVA) when necessary. A generalized linear model, where AC and P were treated as fixed factors, was used. Thus we used a two-way ANOVA to test the effects of these fixed factors on the whole-plant biomass, root biomass, shoot biomass, root N:P ratio, and shoot N:P ratio. Individual means were compared with a *post hoc* Turkey test. Additionally, an independent sample *t*-test was used to test whether the relative change differed between low P and high P. All statistical analyses were carried out with SPSS 19.0 (SPSS Inc., Chicago).

## Results

Across three plant species grown in low and high P conditions, AC addition substantially increased their whole-plant biomass from  $0.69 \pm 0.09$  g (mean  $\pm$  1 SE) to  $1.04 \pm 0.14$  g (Fig. 1a, d, g;  $F = 106.2$ ,  $P < 0.000$ ). Importantly, this AC effect varied with species identity and P levels. For *Lactuca*, AC had no effect on its biomass in the low P, but AC increased its whole-plant biomass, root biomass, and shoot biomass in the high P (Fig. 1a–c; Table 1). For *Sesbania*, AC had no effect on its biomass in the low P, but AC increased its whole-plant biomass, root biomass, and shoot biomass in the high P (Fig. 1d–f; Table 1). For *Solidago*, AC increased its whole-plant biomass, root biomass, and shoot biomass, regardless of in low or high P conditions (Fig. 1g–i; Table 1). P addition increased the whole-plant,

**Table 1** General linear model results about the effects of activated carbon (AC), soil phosphorus (P), and their interactions on the whole-plant biomass, root biomass, shoot biomass, root N:P ratio, and shoot N:P ratio. Values of  $P < 0.05$  are in bold

	Whole-plant biomass		Root biomass		Shoot biomass		Root N:P ratio		Shoot N:P ratio	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Lactuca</i>										
AC	<b>6.489</b>	<b>0.022</b>	2.820	0.114	<b>9.038</b>	<b>0.009</b>	<b>17.43</b>	<b>0.001</b>	0.200	0.661
P	<b>17.20</b>	<b>0.001</b>	<b>7.120</b>	<b>0.018</b>	<b>25.97</b>	<b>&lt;0.000</b>	<b>19.12</b>	<b>0.001</b>	<b>97.62</b>	<b>&lt;0.000</b>
AC × P	<b>5.259</b>	<b>0.037</b>	1.927	0.185	<b>7.887</b>	<b>0.013</b>	1.027	0.327	0.084	0.776
<i>Sesbania</i>										
AC	<b>10.90</b>	<b>0.004</b>	<b>20.06</b>	<b>&lt;0.000</b>	<b>7.479</b>	<b>0.014</b>	<b>7.415</b>	<b>0.016</b>	0.567	0.462
P	<b>18.67</b>	<b>&lt;0.000</b>	<b>12.31</b>	<b>0.003</b>	<b>20.18</b>	<b>&lt;0.000</b>	<b>54.39</b>	<b>&lt;0.000</b>	<b>88.67</b>	<b>&lt;0.000</b>
AC × P	<b>12.80</b>	<b>0.002</b>	<b>10.70</b>	<b>0.005</b>	<b>12.80</b>	<b>0.002</b>	2.668	0.123	2.203	0.157
<i>Solidago</i>										
AC	<b>11.08</b>	<b>0.004</b>	<b>6.694</b>	<b>0.019</b>	<b>12.52</b>	<b>0.003</b>	<b>71.83</b>	<b>&lt;0.000</b>	0.981	0.337
P	1.851	0.191	1.871	0.189	1.746	0.204	<b>39.35</b>	<b>&lt;0.000</b>	<b>109.2</b>	<b>&lt;0.000</b>
AC × P	0.010	0.922	0.309	0.586	0.008	0.932	<b>6.952</b>	<b>0.018</b>	0.062	0.806

root, and shoot biomass of *Lactuca* and *Sesbania*, but not *Solidago* (Fig. 1; Table 1).

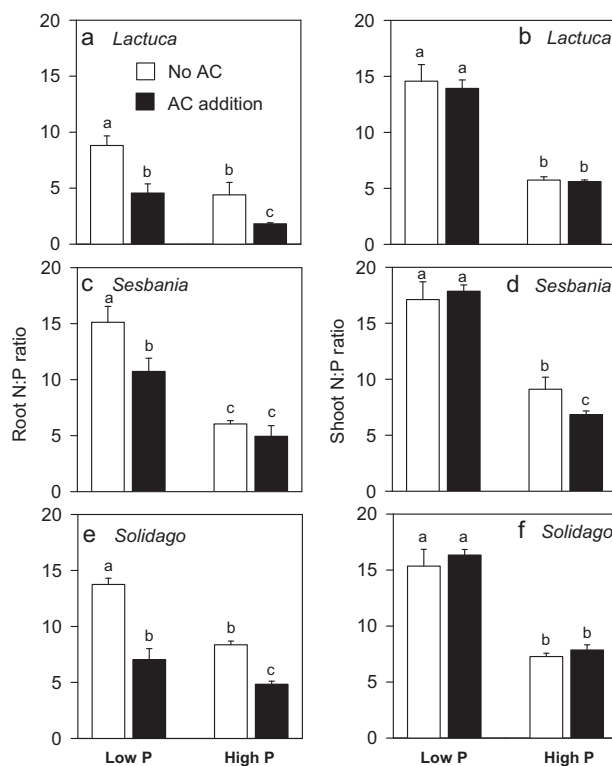
The relative changes in whole-plant biomass, root biomass, and shoot biomass were greater in *Sesbania* than in *Lactuca* and *Solidago* under the high P conditions (Fig. 1; all  $P < 0.05$ ). Interestingly, this relative change in *Solidago* was greater in the low P condition than in the high P condition (Fig. 1g–i; all  $P < 0.05$ ). Additionally, the relative change in biomass due to AC addition differed between roots and shoots, irrespective of species identity (all  $P < 0.05$ ).

Overall, root N:P ratios were more sensitive to AC addition than shoot N:P ratios (Fig. 2; Table 1). That is, AC addition significantly decreased root N:P ratios, but did not alter shoot N:P ratios (Fig. 2a–f; Table 1). P enrichment decreased root N:P ratios and shoot N:P ratios (Fig. 2a–f; Table 1). For *Lactuca* and *Sesbania*, AC and P influenced their root N:P ratios independently; for *Solidago*, AC and P exhibited a significant interaction on its root N:P ratio (Table 1).

## Discussion

We found that AC addition greatly increased plant growth, as indicated by biomass. Thus, the intact root exudates of three species had autotoxicity. In our study this autotoxicity varied with plant species and soil P; our study also provide a possible stoichiometric explanation for autotoxicity. Although these results cannot be simply extrapolated due to limited species and controlled conditions, they add to our understanding of root exudate autotoxicity in the context of plant communities.

The modulation of soil P on root exudate autotoxicity relied on species identity, supporting our first hypothesis.



**Fig. 2** Root N:P ratio and shoot N:P ratio of **a, b** *Lactuca sativa*, **c, d** *Sesbania cannabina*, and **e, f** *Solidago canadensis* grown under four conditions consisting of activated carbon (AC) and soil P. Data are means + 1 SE

This dependence could be associated to the difference in autotoxic costs among different species (Wise and Abrahamson 2017). For *Lactuca* and *Sesbania*, root exudate autotoxicity occurred only in the high P condition. For *Solidago*, root exudate autotoxicity occurred in low and high P conditions; however, this autotoxicity was more pronounced in the low P condition. *Lactuca* and *Sesbania*

grew smaller in low P than in high P, but *Solidago* grew similarly at two P levels. Similar findings have been reported in previous studies (von Elert and Jüttner 1997; Jarchow and Cook 2009). This species-dependent P effect could drive ecological autocatalysis (e.g. species assemblage and community composition and structure) (Veldhuis et al. 2018). This phenomenon could provide an initial indication why these species with contrasting growth forms preferentially occupy different habitats (Editorial Board of Flora of China 1985, 1990). For example, *Lactuca* and *Sesbania* might prefer to occupy low-P microsites in the field whereas *Solidago* might prefer to occupy high-P microsites. *Lactuca* and *Solidago* belong to the same family (i.e. Asteraceae), but their contrasting root exudate autotoxicities might allow them to differentiate spatially. This autotoxicity-driven differentiation, at long-term and larger scales, favors the distribution of species and their coexistence and diversity.

In this study, the low P condition was unfavorable for the plant growth of *Lactuca* and *Sesbania*; soil P enrichment increased the total biomass of plants in the absence of root exudates and more importantly the decreased biomass due to the presence of root exudates was greater in high P than in low P. Therefore, soil P enrichment increased root exudate autotoxicity in *Lactuca* and *Sesbania*, supporting our second hypothesis and agreeing previous findings (Bu et al. 2016, 2018). This P effect on autotoxicity could be ascribed to the following possibilities. First, soil P enrichment decreased the root N:P ratios, implying that the uptake of N and P was disproportionately enhanced when high P was available (Güsewell 2004). Second, decreased root biomass allocation might play an important role in determining this P effect (He Wei-Ming and Sun Zhen-Kai, unpublished data), because this decrease is unbeneficial for plants to acquire soil nutrients (Bloom et al. 1985; Freschet et al. 2018). Third, soil P deficiency can stimulate root exudation (Tharayil et al. 2009; Inderjit et al. 2011), which in turn influences root exudate autotoxicity. These findings might have a few implications for plant communities. For example, root exudate autotoxicity was low when soil P was low, and vice versa. This P-dependent autotoxicity could modulate the spatial patterns of plants through altering intraspecific competition.

Interestingly, AC addition altered root N:P rather than shoot N:P. Based on these data, we proposed a possible explanation (i.e. high N:P ratio inhibition) for root exudate autotoxicity, supporting our third hypothesis. More specifically, intact root exudates suppressed biomass accumulation via increasing root N:P ratios, because root exudates can modulate mineral acquisition (Dakora and Phillips 2002) and N:P ratios can indicate the nutrient acquisition of plants (Güsewell 2004). This possibility could be further

supported by the P enrichment effect above. Autotoxicity might be harmful to crops due to decreasing their yield and quality (Bu et al. 2016, 2018). Unlike crops, autotoxicity might be beneficial to natural communities, particularly at long-term and/or larger scales. This benefit at least includes two aspects. Autotoxicity partly decreases intraspecific competition, because this competition can be intense due to the same resource requirement and acquisition strategies (Crowley 1997). Autotoxicity can also in part decrease interspecific competition through avoiding asymmetric competition among different species (Grace and Tilman 1990).

Additionally, we observed that root exudate autotoxicity differed between roots and shoots. In other words, root exudates differentially inhibited the growth of roots and shoots, thereby exhibit contrasting contributions to the whole-plant inhibition. For annual *Sesbania*, roots played a more important role in whole-plant inhibition than shoots; the opposite was the case for biennial *Lactuca*. For *Solidago*, roots played a more important role in whole-plant inhibition than shoots in the low P, and the opposite was true in the high P. Taken together, these findings suggest that root exudates show autotoxicity through multiple pathways.

In summary, our experiment showed that soil P availability strongly mediated root exudate autotoxicity and this P effect depended tightly on species identity. These findings might help us to better understand the ecological role of root exudate autotoxicity. This P-mediated species-specific autotoxicity might be important for higher level organization. Although the need to study root exudate autotoxicity has been widely recognized (Rice 1974; Munther and Fairbrothers 1980; Perry et al. 2005; Bauer et al. 2012; Chen et al. 2014; Bu et al. 2016, 2018), the following aspects still deserve increasing attention. First, a broad range of plant species differing in growth forms and habits should be screened to achieve a more general conclusion. Second, root exudate autotoxicity should be in situ examined using new techniques otherwise we cannot obtain a realistic picture. Finally, it is required to consider the role of various soil microbial fractions, because they can influence the mineral nutrition of plants, and are also a crucial factor determining root exudate autotoxicity through external pathways (Zabinski et al. 2002; van der Putten et al. 2016).

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This work does not contain any studies with human participants performed by any of the authors. All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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