

## Soil organic nitrogen endows invasive *Solidago canadensis* with greater advantages in low-phosphorus conditions

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**Abstract.** Although the importance of soil nitrogen (N) and phosphorus (P) has long been recognized in plant nutrition, no study has addressed how soil organic N and P contribute to the success of invasive plants. To do so, we conducted two experiments in which invasive *Solidago canadensis* and native *S. decurrens* were either subjected to five amino acids or subjected to organic and inorganic N treatments (i.e., five amino acids and five ratios of nitrate to ammonium) under two P levels. In the first experiment, *S. canadensis* and *S. decurrens* grew taller when five amino acids were supplied than when no N was supplied, suggesting both species can use soil amino acids as N sources. In a second experiment, *S. canadensis* grew larger and taller than *S. decurrens* in the presence of organic and inorganic N, and organic N exhibited greater positive effects on the growth advantage of *S. canadensis* relative to *S. decurrens* than inorganic N; P levels influenced the effects of organic N on plant growth through changing biomass allocation and leaf chlorophyll. These results suggest that organic N and inorganic N may differentially contribute to the growth advantage of invasive species. Considering plant organic N economy is necessary to elucidate invasion mechanisms and expand plant strategies.

**Key words:** growth advantages; invasion mechanisms; nitrogen forms; phosphorus availability; *Solidago canadensis*.

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### INTRODUCTION

The classical paradigm of plant N economy assumes that terrestrial plants use only inorganic N (i.e., nitrate and ammonium) (Chapin 1980, Schimel and Bennett 2004). However, this paradigm has been increasingly challenged for the last 20 yr because some mycorrhizal and non-mycorrhizal plants can take up soil organic N (Näsholm et al. 2009). For example, some plants of the arctic tundra (Chapin et al. 1993, Kielland 1994, Schimel and Chapin 1996, Jonasson and Shaver 1999, McKane et al. 2002), boreal forests

(Näsholm et al. 1998, Jonasson and Shaver 1999), alpine and subalpine steppes (Raab et al. 1999), and temperate grasslands (Näsholm et al. 2000, Bardgett et al. 2003, Weigelt et al. 2005, Harrison et al. 2008) have been shown to take up and utilize amino acids as a N source. These studies have advanced our understanding of plant N nutrition. However, no study has addressed organic N nutrition in invasive plants. This gap motivates us to answer a fundamental question: can invasive plants use soil amino acids?

Some studies have suggested that the capacity of native plants to absorb amino acids is

correlated with their molecular mass and this correlation may be linked to the configuration and complexity of amino acids (Kielland 1994, Harrison et al. 2007). By the same token, if invasive plants can use soil amino acids, then they also might exhibit a preference for amino acids. Accordingly, we attempted to test whether there are significant correlations between plant growth and the molecular mass of amino acids.

Large amounts of P are required to sustain plant growth and metabolism and soil P is a growth-limiting nutrient in many natural ecosystems (Chapin 1980, Aerts and Chapin 2000, Elser et al. 2007). Soil P limitation also can influence the uptake and use of inorganic N by terrestrial plants, thereby playing important roles (Chapin 1980, Aerts and Chapin 2000, Gusewell 2004, Elser et al. 2007). *Solidago canadensis* commonly invades diverse habitats (Dong et al. 2006), where soil P availability fluctuates dramatically. No studies to date have addressed whether soil P availability modulates the organic N nutrition of invasive plants. Given that soil P can influence inorganic N nutrition (Chapin 1980, Aerts and Chapin 2000, Gusewell 2004, Elser et al. 2007), soil P levels also may modulate the organic N nutrition of invasive plants.

In natural ecosystems, inorganic N and organic N exist simultaneously (Harrison et al. 2007, 2008), and nitrate and ammonium constitute a small proportion of bio-available soluble N in the soil solution and amino acids dominate over inorganic N (Näsholm et al. 2009, Schmidt et al. 2014, Warren 2014). Such phenomena also occur in some areas invaded by *S. canadensis* (Hou et al. 2009, Appendices Fig. A1). Here, we hypothesized that organic N and inorganic N differentially contribute to the growth advantage of invaders, because the uptake of organic and inorganic N has different mechanisms (Forde 2000, Howitt and Udvardi 2000, Näsholm et al. 2009).

In nature, the ratios of nitrate to ammonium are variable (Chapin 1980, Stevens et al. 2010). This change can alter both the availability of inorganic N and environmental conditions (e.g., soil pH) (cf. Stevens et al. 2010), which in turn affect plant growth and distribution (Chapin 1980, Stevens et al. 2010). Successful invaders usually occupy diverse habitats, where the ratios of nitrate to ammonium are variable dramatically.

This pattern suggests that successful invaders can adapt to diverse inorganic N conditions.

In this study, we conducted two complementary experiments. In the first experiment, *S. canadensis* and *S. decurrens* were subjected to five amino acids and the control (i.e., no N addition), and plant height was measured as a proxy of plant growth. In a second experiment, *S. canadensis* and *S. decurrens* were subjected to five amino acids and five ratios of nitrate to ammonium under two P levels, and total biomass, plant height, root biomass allocation, leaf area, and leaf chlorophyll were determined. Total biomass and plant height can indicate plant growth. Root biomass allocation, leaf area, and leaf chlorophyll can provide possible explanations for the differences of individuals between organic and inorganic N, because roots and leaves, which influence plant performance, are two fundamental interfaces between plants and their environments.

## MATERIALS AND METHODS

### Study species

*Solidago canadensis* is native to North America, and is a worldwide invader in Europe, large parts of Asia, Australia, and New Zealand (Weber 2003). *Solidago canadensis* was introduced into China in 1935, and now invades roadsides, abandoned fields, agricultural fields, and pastures (Dong et al. 2006). *Solidago decurrens* is native to China and a common forb. These two species are patchily distributed in some cases, and the seeds of each species were collected from five populations for the following experiments.

### Growth experiment I

We used a mixture of 1:1 sand and vermiculite, both of which were gamma sterilized to 40 kGy. All experimental plants from seed were grown in 250-mL pots filled with the above mixture (one individual per pot). Note that the mixture was sterilized to minimize the effects of soil microbes in N transformations and to test whether added amino acids can be used by plants directly. We set up six treatments: control (i.e., no N addition), arginine (Arg; molecular mass [MM] = 174), glutamic acid (Glu; MM = 147), glycine (Gly; MM = 75), proline (Pro; MM = 115), and tryptophan (Trp; MM = 204). We based amino acid treatments

on our work (see Appendices Fig. A1). These amino acids represent a gradient of MM and have different configurations and complexities. We supplemented these five amino acids in aqueous solution corresponding to 20 mg N per kg soil, and the control pots received water only.

Experimental plants from *S. canadensis* or *S. decurrens* were assigned to each of the six treatments. All the pots were placed in a greenhouse and rotated every week to avoid the possible effects of micro-site variability. During the experiment, all plants were watered as required to be sure that larger plants did not become relatively more water-limited than smaller plants, and N loss did not occur. The experiment lasted three months, and each treatment included 10 replicates. Finally, we determined the height of all plants. To quantify the relative effects of amino acids, we calculated the relative increase in plant height (RIPH):  $RIPH = (H_{Aa} - H_{control}) / H_{control} \times 100\%$ , where  $H_{Aa}$  and  $H_{control}$  are the plant height of *S. canadensis* and *S. decurrens* grown in a given amino acid and the control. We used a one-way analysis of variance (ANOVA) to test the difference in plant height/RIPH among N treatments or between two species. Correlation analysis was used to test the relationships between plant height and the molecular mass of amino acids.

### Growth experiment 2

We conducted a second growth experiment. Our goals were to address how the effects of N forms are dependent on soil P availability. We set up 10 N treatments: five amino acids (Arg, Glu, Gly, Pro, and Trp) and five  $NO_3^-:NH_4^+$  ratios. We based amino acid treatments on our work (see Appendices Fig. A1) and other work (Hou et al. 2009). In 2014, we collected soil samples from 220 sites and found that  $NO_3^-:NH_4^+$  ratios changed dramatically across the invaded range by *S. canadensis* (see Appendices Fig. A2). Accordingly, we set up five  $NO_3^-:NH_4^+$  ratios (100:0, 75:25, 50:50, 25:75, 0:100) based on our work, representing five scenarios of inorganic N. We selected  $NaNO_3$  as nitrate-N and  $NH_4Cl$  as ammonium-N. We supplemented organic N and inorganic N in aqueous solution in three applications totaling 50 mg N per kg soil. During the experiment, all plants were supplied with the modified

Hoagland's nutrient solution (i.e., no N). To examine the effect of P availability on plant N nutrition, we set up two P levels. In the low P, no additional P was supplied. In the high P, we supplemented P, as  $P_2O_5$ , in aqueous solution in three applications totaling 10 mg P per kg soil. Taken together, there were 20 combinations of N and P treatments.

We used the mixture of 1:1 sand and vermiculite, both of which were gamma sterilized to 40 kGy. Accordingly, we could maximize to exclude the effects of soil microbes in N transformations and test whether added amino acids can be used by plants directly. Experimental plants from *S. canadensis* or *S. decurrens* were grown in 250-mL pots (one individual per pot) filled with the mixture and assigned to each of the 20 combinations. All the pots were placed in a greenhouse and rotated every week to avoid the possible effects of micro-site variability. During the experiment, all plants were watered as required to be sure that larger plants did not become relatively more water-limited than smaller plants, and nutrient loss did not occur. The experiment ran from late June to early October 2014, and each treatment included eight replicates (320 pots in total). Finally, plant height was measured with a ruler and leaf chlorophyll was determined with the SPAD meter; all experimental plants were harvested, separated into roots, leaves, and other aboveground parts. The total leaf area per plant was determined with the WinRhizo system. All samples were oven-dried at 75 °C for 48 h and weighed.

Root biomass allocation (RBA) was calculated:  $RBA = \text{root dry biomass} / \text{total dry biomass} \times 100\%$ . To quantify the performance difference between invasive and native species, we calculated the relative change in plant traits (RCPT):  $RCPT = (Sc - Sd) / Sd \times 100\%$ , where Sc and Sd are the total biomass, plant height, RBA, total leaf area, and leaf chlorophyll of *S. canadensis* and *S. decurrens* grown in a given combination of N and P.

For total biomass, plant height, RBA, total leaf area, and leaf chlorophyll, we used the linear mixed model within SPSS, where species, N form, and P availability were treated as fixed factors and each N treatment nested within organic N or inorganic N was treated as a random factor, to test the effects of these factors and their interactions on the above five traits. For the relative

changes in total biomass, plant height, RBA, total leaf area, and leaf chlorophyll, the related data were pooled together across five amino acid treatments or across five ratios of nitrate to ammonium. We used the general linear mixed model within SPSS, where N forms and P availability were treated as fixed factors, to test the effect of those factors and their interactions on the above relative changes. Correlation analysis was used to test the relationships between total biomass and the molecular mass of amino acids.

## RESULTS

### Experiment 1

Invasive *S. canadensis* and native *S. decurrens* grew much taller when five amino acids were supplied than when no N was supplied (Fig. 1;

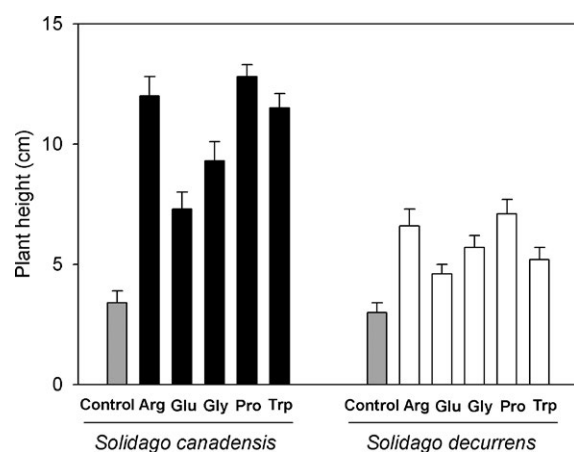


Fig. 1. Plant height of *Solidago canadensis* and *S. decurrens* grown in six treatments. In the control no N was added. Arg: arginine; Glu: glutamic acid; Gly: glycine; Pro: proline; Trp: tryptophan. Data are means + 1 SE.

all  $P < 0.001$ ). *Solidago canadensis* ( $10.6 \pm 1.3$  cm [1 SE]) grew taller than *S. decurrens* ( $5.8 \pm 0.7$  cm) and the relative increase of *S. canadensis* ( $210 \pm 15\%$ ) was greater than that of *S. decurrens* ( $95 \pm 12\%$ ) (Fig. 1; all  $P < 0.001$ ). The plant height of each species was not correlated with the molecular mass of amino acids (all  $P > 0.05$ ).

### Experiment 2

Overall, *S. canadensis* grew larger than *S. decurrens*, and organic N and high P enhanced the growth of *Solidago* species (Table 1: all  $P < 0.001$ ; Fig. 2). *Solidago canadensis* produced more biomass in the organic N than in the inorganic N ( $P < 0.001$ ;  $2.92 \pm 0.07$  g vs.  $2.43 \pm 0.07$  g), and *S. decurrens* produced the same biomass in organic and inorganic N conditions ( $P = 0.169$ ;  $2.00 \pm 0.07$  g vs.  $1.86 \pm 0.08$  g). Accordingly, organic N had a greater contribution to *S. canadensis* growth compared to *S. decurrens* than inorganic N (Table 2;  $49 \pm 3\%$  vs.  $38 \pm 4\%$ ). More importantly, for *S. canadensis* N forms and P availability together determined its relative increase in biomass (Table 2). Specifically, organic N had a stronger positive effect on the growth advantage of *S. canadensis* than inorganic N in the low-P condition (small panel in Fig. 2a), and organic and inorganic N exhibited similar effects on its growth advantage in the high-P condition (small panel in Fig. 2b). Additionally, the total biomass of each species was not correlated with the molecular mass of amino acids, regardless of low-P or high-P conditions (all  $P > 0.05$ ).

In any conditions, *S. canadensis* grew much taller than *S. decurrens*; organic N and high P increased the height of *Solidago* species (Table 1: all

Table 1. Analysis of variance of total biomass, plant height, root biomass allocation (RBA), total leaf area, and leaf chlorophyll. Values of  $P < 0.05$  are in bold.

	Species (S)	Nitrogen (N)	Phosphorus (P)	S × N	S × P	N × P
	P	P	P	P	P	P
Total biomass	<0.001	<0.001	<0.001	<0.001	0.650	<0.001
Plant height	<0.001	<b>0.027</b>	<0.001	<b>0.001</b>	<0.001	<0.001
RBA	<0.001	<0.001	0.702	0.835	<b>0.001</b>	0.204
Leaf area	<0.001	0.856	<0.001	<b>0.005</b>	<b>0.007</b>	0.413
Chlorophyll	<0.001	0.842	<0.001	<b>0.016</b>	<b>0.001</b>	0.311

$P < 0.05$ ; Fig. 3). Across two levels of P, organic N had stronger positive effects on *S. canadensis* height than inorganic N (Table 2; small panels in

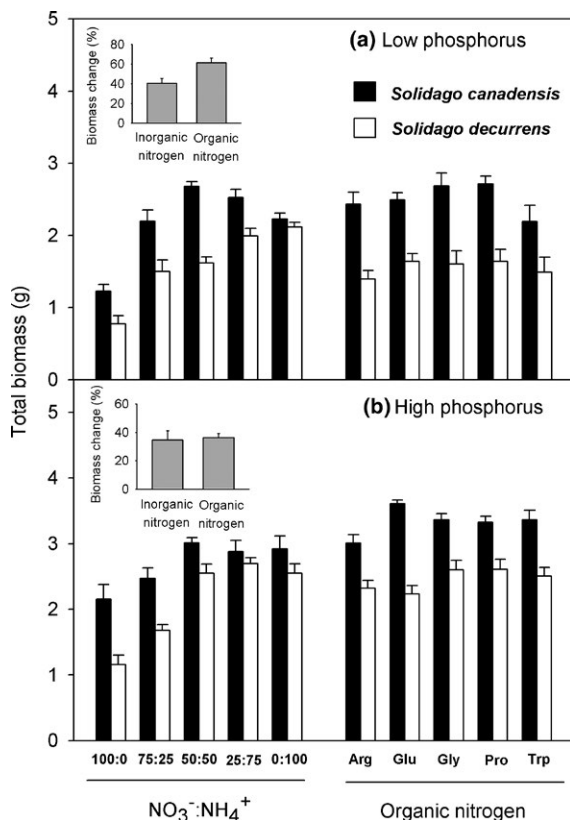


Fig. 2. Total biomass of *Solidago canadensis* and *S. decurrens* grown in inorganic and organic N conditions with low P (a) or high P (b). The relative changes in the total biomass of *S. canadensis* compared to *S. decurrens* in inorganic and organic N conditions are presented in small panels, and see text for detailed calculation. Data are means + 1 SE.

Fig. 3). Like total biomass, organic N conferred a stronger positive effect on the height advantage of *S. canadensis* than inorganic N in the low-P condition (small panel in Fig. 3a), and organic and inorganic N had similar effects on its height advantage in the high-P condition (small panel in Fig. 3b).

*Solidago canadensis* allocated less biomass to its roots than *S. decurrens*, and root biomass allocation (RBA) was greater in the organic N than in inorganic N across two species (Table 1: all  $P < 0.001$ ; Fig. 4). Although N forms alone did not affect the relative change in RBA of *S. canadensis*, its interaction with P followed the opposite direction (Table 2). For example, organic N had a weaker effect on decreased RBA of *S. canadensis* than inorganic N in the low-P condition (small panel in Fig. 4a), and organic and inorganic N equally affected this decrease in the high-P condition (small panel in Fig. 4b).

*Solidago canadensis* had greater leaf area and higher chlorophyll than *S. decurrens* across all N and P treatments, and leaf area and chlorophyll of *Solidago* species varied with P levels (Table 1: all  $P < 0.001$ ; Figs. 5 & 6). Organic N had a stronger positive effect on the relative increase in the leaf area of *S. canadensis* than inorganic N across two levels of P (Table 2; Fig. 5:  $43 \pm 3\%$  vs.  $34 \pm 4\%$ ), but this effect was independent of P availability (Table 2; small panels in Fig. 5a & b). For *S. canadensis* the relative increases in chlorophyll were sensitive to N forms, P levels, and their interactions (Table 2: all  $P < 0.001$ ). In the low-P condition organic and inorganic N equally affected the relative increase in the chlorophyll of *S. canadensis* (Fig. 6a), and organic N had smaller effects on this increase than inorganic N in the high-P condition (Fig. 6b:  $5 \pm 1\%$  vs.  $12 \pm 1\%$ ).

Table 2. Analysis of variance of the relative changes in the total biomass, plant height, root biomass allocation, total leaf area, and leaf chlorophyll in *Solidago canadensis* (% of the *S. decurrens*). Values of  $P < 0.05$  are in bold.

	Nitrogen (N)		Phosphorus (P)		N × P	
	F	P	F	P	F	P
Relative change in total biomass	6.942	<b>0.009</b>	13.104	<b>&lt;0.001</b>	4.901	<b>0.028</b>
Relative change in plant height	12.483	<b>0.001</b>	0.548	0.460	3.517	0.063
Relative change in root biomass allocation	0.632	0.428	25.472	<b>&lt;0.001</b>	17.831	<b>&lt;0.001</b>
Relative change in total leaf area	4.755	<b>0.031</b>	41.541	<b>&lt;0.001</b>	0.175	0.676
Relative change in leaf chlorophyll	13.943	<b>&lt;0.001</b>	28.333	<b>&lt;0.001</b>	13.651	<b>&lt;0.001</b>

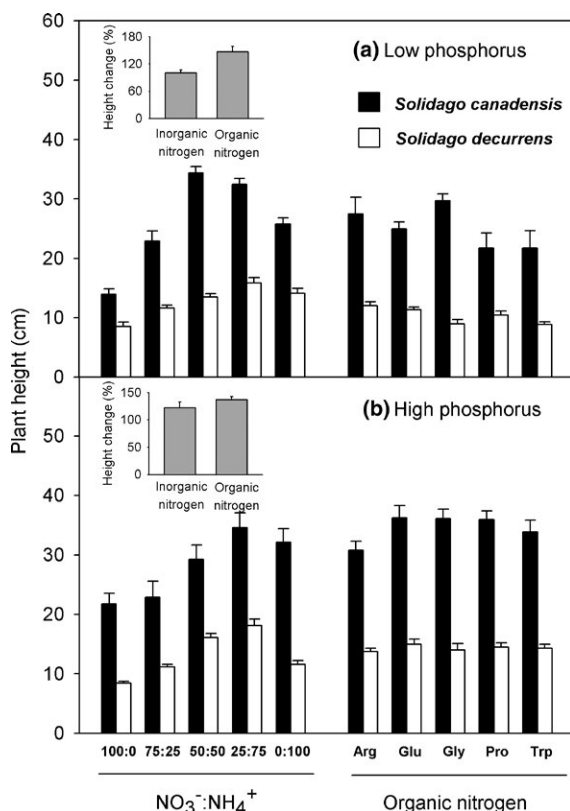


Fig. 3. Plant height of *Solidago canadensis* and *S. decurrens* grown in inorganic and organic N conditions with low P (a) or high P (b). The relative changes in the plant height of *S. canadensis* compared to *S. decurrens* in inorganic and organic N conditions are presented in small panels, and see text for detailed calculation. Data are means + 1 SE.

## DISCUSSION

The first key finding of our study was that invasive *S. canadensis* had access to amino acids as N sources. Specifically, *S. canadensis* grew larger/higher when organic N was supplied than when no N was supplied or inorganic N was supplied. Our work suggests that some invaders may take up and utilize soil organic N, particularly in habitats rich in free amino acids. If organic N uptake is widespread in invasive plants, then this process short-circuits the mineralization step and has important ramifications for our understanding of plant N nutrition, especially as previous studies on plant N nutrition focus entirely on the availability and plant uptake of inorganic N.

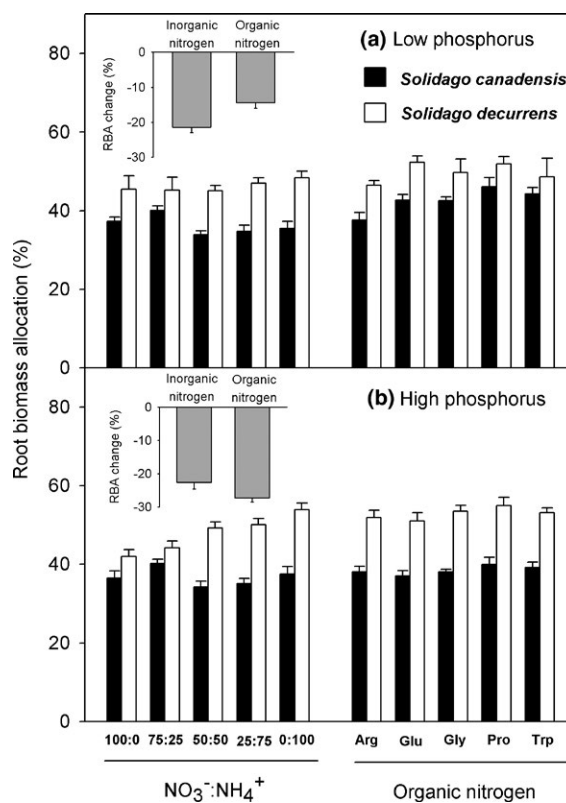


Fig. 4. Root biomass allocation (RBA) of *Solidago canadensis* and *S. decurrens* grown in inorganic and organic N conditions with low P (a) or high P (b). The relative changes in RBA of *S. canadensis* compared to *S. decurrens* in inorganic and organic N conditions are presented in small panels, and see text for detailed calculation. Data are means + 1 SE.

Previous researchers used three amino acids and found that the capacity of plants to absorb amino acids was negatively correlated with their molecular mass (Kielland 1994, Harrison et al. 2007). If this is ubiquitous, then biomass production or plant height seems to decline with increasing molecular mass of amino acids. We used five amino acids (ranging from the smallest molecular mass to the largest molecular mass) in our two experiments, but did not find significant correlations between biomass/plant height and the molecular mass of five amino acids, regardless of *S. canadensis* or *S. decurrens*. Accordingly, the molecular mass of amino acids does not necessarily indicate their potential to be taken up by plants, and other attributes of amino acids (e.g., configuration and acidity)

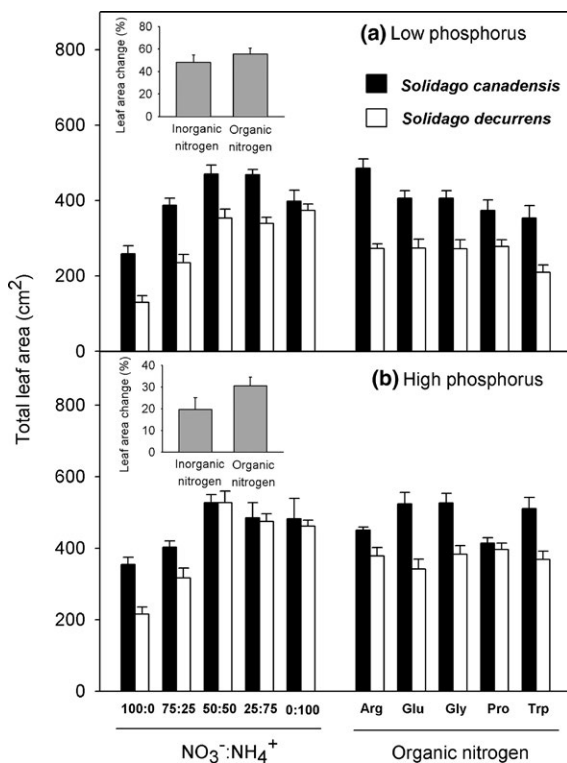


Fig. 5. Total leaf area of *Solidago canadensis* and *S. decurrens* grown in inorganic and organic N conditions with low P (a) or high P (b). The relative changes in the total leaf area of *S. canadensis* compared to *S. decurrens* in inorganic and organic N conditions are presented in small panels, and see text for detailed calculation. Data are means + 1 SE.

may be crucial to govern amino acid uptake. In other words, the selective uptake of soil amino acids cannot be attributed to their molecular mass simply.

The molecular mechanisms of amino acid uptake have been elucidated in noninvasive plants, especially in *Arabidopsis thaliana* (Bush 1993, Fischer et al. 1998, Näsholm et al. 2009, Paungfoo-Lonhienne et al. 2012). However, we do not know the exact processes of amino acid uptake in invasive plants so that this issue deserves thorough studies in the future. There were substantial variations in growth, biomass allocation, and leaf traits among five amino acids. This suggests that *S. canadensis* differentially takes up soil amino acids. Such phenomenon has been found in previous studies with nonnative plants (Kielland 1994, Weigelt et al. 2005), and may be linked to

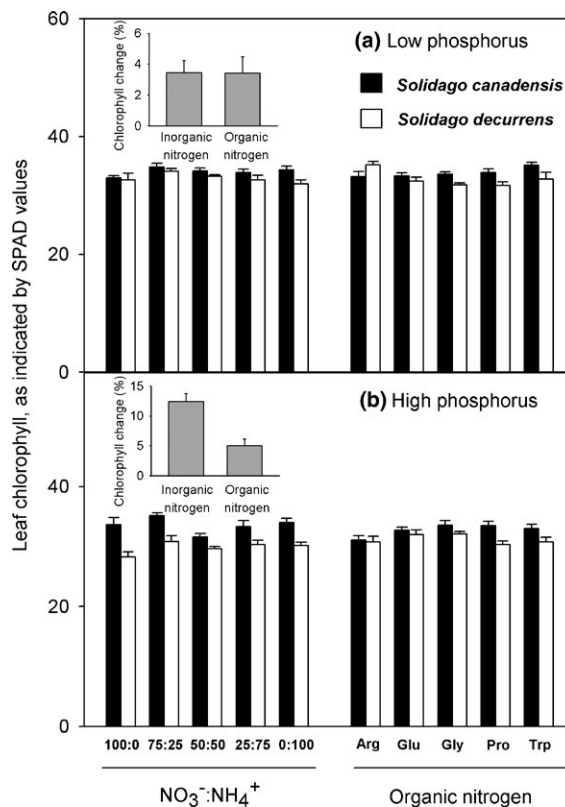


Fig. 6. Leaf chlorophyll, as indicated by SPAD values, of *Solidago canadensis* and *S. decurrens* grown in inorganic and organic N conditions with low P (a) or high P (b). The relative changes in the chlorophyll of *S. canadensis* compared to *S. decurrens* in inorganic and organic N conditions are presented in small panels, and see text for detailed calculation. Data are means + 1 SE.

organic N transporters (Bush 1993, Fischer et al. 1998, Näsholm et al. 2009, Paungfoo-Lonhienne et al. 2012).

The novel contribution of our results is that P availability regulated the effects of organic N on the performance of *S. canadensis*. Accordingly, *S. canadensis* performed differently in low- vs. high-P conditions. This finding expands the prevailing notion that N uptake is linked to the availability of other nutrients (Schmidt et al. 2014). Here, we propose a couple of hypotheses that might explain our results. First, compared with *S. decurrens*, *S. canadensis* allocated less biomass to its roots, regardless of inorganic or inorganic N conditions; this decrease varied with soil P availability. For example, when low

P was supplied, *S. canadensis* allocated more biomass to its roots in the presence of organic N than in the presence of inorganic N, thereby enhancing plant N uptake. Overall, changing biomass allocation is widely recognized as a strategy for plants to cope with variable habitats (Chapin 1980, Aerts and Chapin 2000). Second, soil P modulates the effects of organic N on plant growth through changing leaf chlorophyll rather than total leaf area. Specifically, organic and inorganic N had the same effects on the relative increase in leaf area, regardless of in low- or high-P conditions; however, the opposite was the case for chlorophyll. Finally, soil N and P together determined plant shoot, which in turn regulates plant N absorption (i.e., so-called shoot-derived signals, Forde and Clarkson 1999). Accordingly, soil organic N acts in concert with soil P to help *S. canadensis* grow larger and higher.

A second key finding of our study was that the absolute and relative increases in *S. canadensis* growth were greater across five amino acids than across five ratios of nitrate to ammonium, thereby suggesting that organic N contributes to the growth advantage of *S. canadensis* more than inorganic N. Additionally, organic and inorganic N conferred different effects on biomass allocation and leaf traits. There are a few possible explanations for these differential effects. First, organic N is taken up through organic N transporters (Bush 1993, Fischer et al. 1998, Näsholm et al. 2009, Paungfoo-Lonhienne et al. 2012), while inorganic N is absorbed by virtue of nitrate or ammonium transporters (Forde 2000, Howitt and Udvardi 2000). In other words, there are differences in molecular mechanisms between organic and inorganic N uptake. Second, *S. canadensis* commonly has a mycorrhizal association in the field (Dong et al. 2006), which can enhance the organic N uptake of plants (Kielland 1994, Näsholm et al. 2009). Thus, *S. canadensis* takes up amino acids through both direct and indirect pathways while does inorganic N via direct pathways only. Additionally, we suspect that differential uptake may be linked to root traits including specific root length, root hair, and architectures, because N forms can regulate these root traits (Forde and Clarkson 1999, Aerts and Chapin 2000). Thus, organic N has a

greater contribution to the growth advantage of *S. canadensis* than inorganic N.

N losses did not occur through supplying adequate water, although organic N and inorganic N may have different capacities to leach from soil due to the differences in composition and structure. Obviously addressing this leaching capacity is beyond the scope of our study. In the field, soil organic N dominates over inorganic N (Näsholm et al. 2009, Schmidt et al. 2014, Warren 2014). This was true in the range invaded by *S. canadensis*. If invasive plants have access to a broader spectrum of N sources, then they may decrease competition with some native plants lacking this access. This N differentiation can explain, to some extent, why plant invasion does not always reduce native plant species richness (Gaertner et al. 2009, Ricciardi et al. 2013). Soil amino acids enhanced the growth advantage of *S. canadensis*, particularly in the presence of low P. This advantage has important implications. For example, the superior growth of *S. canadensis* is likely to enable it more competitive, and growing taller allows *S. canadensis* to easily shade other local plant species.

We found that the ratios of nitrate to ammonium had profound effects on the growth, biomass allocation, and chlorophyll of *S. canadensis* and *S. decurrens* and that these two species exhibited contrasting responses to changing ratios of nitrate to ammonium. These differences appear to be linked to the transporters of nitrate and ammonium (Forde 2000, Howitt and Udvardi 2000). In nature, many plants can utilize nitrate and ammonium selectively (Forde 2000, Howitt and Udvardi 2000), thereby adapting to diverse N environments (Aerts and Chapin 2000). Accordingly, our results suggest that both species exhibit differentiation in using inorganic N. More importantly, *S. canadensis* grew better than *S. decurrens* in the five ratios of nitrate to ammonium, allowing the former to have stronger adaptation than the latter.

However, it should be noted that *S. canadensis* is a long-lived clonal plant and clonal growth is among the important reproduction ways, particularly after establishment. Our work was short-term experiments and did not link N nutrition and plant clonality so that our results cannot be extrapolated to field conditions simply.



Accordingly, future further studies should consider N nutritional strategies, specific habitat regimes, and plant clonality together.

In summary, our findings suggest that organic N contributes to the outperformance of *S. canadensis* more than inorganic N and that these differential contributions depend on soil P availability. Our findings also highlight the importance of soil organic N in plant invasions, particularly in low-P environments. The generality of our results needs to be further tested with a range of invasive plants. Organic N and inorganic N constitute a broad spectrum of N sources, and thorough study of comparative N economy in invasive plants would not only help us to better understand invasion mechanisms but also expand plant strategies.

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W.-M. He conceived the study and conducted its design, data analysis, and manuscript preparation. H.-W. Yu, J.-X. Yang, and Y. Gao conducted the experiments and assisted with data analysis and writing. We thank Li-Jia Dong for her help in the course of the experiment. This study was supported by two grants from the National Natural Science Foundation of China (31570538) and the Ministry of Science and Technology of China (2015BAC02B05).

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