Soil Biology and Biochemistry 138 (2019) 107594

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Polyploidy in invasive *Solidago canadensis* increased plant nitrogen uptake, and abundance and activity of microbes and nematodes in soil

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ARTICLE INFO

Keywords:
Invasive species
Solidago canadensis
Microbes
Nematodes
Polyploidization
Nitrogen

ABSTRACT

Polyploidization (i.e., multiplication of genome size) is a major driver of plant evolution and is believed to play a significant role in plant invasion. One hypothesis states that polyploids possess larger root systems with increased root exudation and thus, induce a greater effect on the rhizosphere compared to their diploids counterparts. Few experiments, however, have explicitly tested the impacts of the polyploidy of plants on soil organisms in the field. Using a common garden approach, we examined the impacts of native and introduced populations of *Solidago canadensis* with differing ploids (diploid, tetraploid and hexaploid) on soil microbes, nematodes, and carbon (C) - nitrogen (N) turnover. Polyploidy generally increased microbial biomass in soil: while the biomass of all microbial groups was significantly higher under introduced than native tetra- and hexaploids, there was no significant difference in soil bacteria, fungi, and actinomycetes between diploids of the native and introduced populations. The effect of polyploids on soil microbial biomass was greater in November than July, suggesting that the effect becomes stronger later in the growing season. The impact of polyploidy on nematodes was largely dependent on trophic status; polyploids did not significantly affect bacterivores or omnivores + carnivores, but tended to increase the abundance of fungivores, and significantly increased the number of herbivores. Extraradical biomass of arbuscular mycorrhizal fungi was significantly higher, but NO_3^--N and the net nitrification rate were significantly lower under tetra- and hexa-ploids than diploids. Together, these results suggest that polyploidization induces rhizosphere processes that improve plant nutrition and contribute to plant invasiveness through stimulation of soil microbial biomass and increased biological activity.

1. Introduction

Exotic plants threaten the integrity of ecosystems throughout the world (Tyser and Key, 1988; Pimentel et al., 2000; Weber, 2017). Although many invasive species are not dominant in their native habitats, they often out-compete their new neighbors in invaded habitats (Weber, 2017). Several non-mutually exclusive hypotheses have been proposed to explain why plants become invasive in new habitats, including enemy release, evolution of novel traits, disturbance, emergence of novel biochemical weapons, and creation of empty niches in invaded communities (Mack et al., 2000; Hierro et al., 2005; Reinhart and Callaway, 2006; Callaway, 2004, 2008). However, no single mechanism is able explain the invasiveness in different plants, suggesting that the process of invasion may be attributed to a strong selection pressure, leading to a combination of traits contributing to plant invasiveness.

Multiplication of genome size (polyploidy) is a pervasive phenomenon among invasive plants (Marchant et al., 2005). Polyploids are often larger (i.e., biomass production and reproductive output) and more competitive than diploids (Daehler, 2003; Colautti et al., 2006; Pyšek and Richardson, 2008; Thébault et al., 2011). Competitiveness can arise from a small number of functional traits linked to light capture, biomass production and nutrient acquisition (Goldberg and Landa, 1991; Westoby, 1998; Keddy et al., 1998; Thébault et al., 2011). Vegetative traits such as plant height and lateral canopy spread are indicative of plant competition for light and space, respectively (Grime, 1977; Hodáňová, 1981). Classical studies in evolutionary ecology have often focused on variation in above-ground vegetative traits. Consequently, few have investigated the effects of polyploids on plant-soil-microbe interactions, and soil biology (Nash et al., 2003; Silvertown,

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https://doi.org/10.1016/j.soilbio.2019.107594
Received 30 April 2019; Received in revised form 4 September 2019; Accepted 6 September 2019
Available online 06 September 2019
0038-0717/

2004). Understanding how different genotypes of invasive plants affect plant-soil-microbe interactions may provide new insights into mechanisms explaining the invasiveness of polyploids.

Invasive plants may induce changes in below-ground communities and soil nutrient cycling (Bradford et al., 2012). When invasive plants enter new areas, they can directly alter the rhizosphere steady-state (Bever et al., 1997; Bever, 2002, 2003; Parker, 2001), feeding back to plant performance (Augspurger and Kelly, 1984). Invasive plants often exhibit increased root growth to compete with other plants in the introduced range (Lopez-Zamora et al., 2004), increasing C inputs belowground as dead roots and/or root exudates. As microbes are often C-limited (Wardle, 1992), increased C inputs can enhance microbial growth and hence resources for microbial predators, leading to a microbial loop of N cycling (Bonkowski, 2004) that feeds back to the growth of the invasive plant. This positive feedback may be stronger under polyploid plants as they often have larger root systems and more photosynthetic products than their diploid counterparts (Ranney, 2006). Polyploids are more productive and competitive than diploids in nutrient-rich environments (Leitch and Leitch, 2008) and are pre-adapted to the conditions in the new range, providing them with survival and fitness advantages. Polyploid plants have greater genetic diversity and flexibility in their expression of genes, which help facilitate the 'evolution of invasiveness' (Thébault et al., 2011; Birchler, 2012). However, how the polyploidy of invasive plants affects rhizosphere processes remains largely unresolved.

We used *Solidago canadensis* (Canada goldenrod; Wagenitz, 1964), a North American native forb that is highly invasive in China, to examine the potential impact of different polyploids on soil microbial abundance and activity in a common garden experiment. *Solidago canadensis* was originally introduced as an ornamental plant in Shanghai in 1935 (Lu et al., 2007; Weber, 2017), and later escaped causing the current invasion. It shows high genetic variability and different ploidies, or cytotypes (diploid genotypes $2x = 18$, tetraploid genotypes $4x = 36$, hexaploid genotypes $6x = 54$) (Van Kleunen and Schmid, 2003).

Previous experiments have shown that tetra- and hexa-ploids were more competitive against local species than diploids (J. Cheng and S. Qiang, unpublished data, 2019), but how they influence below-ground biology has not been examined. We hypothesized that 1) polyploids, compared to their diploid ancestors, have larger root systems and allocate more resources to soil microbes, thereby increasing soil microbial biomass and activity, while reducing soil extractable N by enhancing plant N uptake, and 2) tetra- and hexa-ploids increase the abundance of bacterial- and fungal-feeding nematodes, and particularly phytophagous nematodes in the soil because of increased C allocation below-ground (i.e., the bottom-up control).

2. Materials and methods

2.1. Study site

A field experiment was established in 2011 at the Pailou Teaching Station of Nanjing Agricultural University (118°37′E, 32°02′N), Nanjing, China. The climate in this region is warm and humid, with an average annual precipitation of 1090.4 mm per year and a mean annual temperature of 15 °C (lowest in February: 2.7 °C, and highest in July: 28.1 °C).

2.2. Experimental design

Experimental field plots were arranged in a two-way factorial block design with origin (native and introduced) and ploidy ($2x$, $4x$ and $6x$) of *S. canadensis* as factors and four replicates allocated to the different blocks (Fig. S1a). Six different genotypes of *S. canadensis* were used: native diploid (NA2x), introduced diploid (IN2x), native tetraploid (NA4x), introduced tetraploid (IN4x), native hexaploid (NA6x) and introduced hexaploid (IN6x) plants (Table S1).

Seeds were germinated and grown in the greenhouse for four months before the seedlings were transplanted to the field. In March 2011, seeds from 72 maternal plants of 18 populations were germinated in pots (11 cm diameter, 8 cm deep, 1 L) with 1:2 mixtures of soil (from the experimental site) and sterilized compost. The pots with plants were placed in a greenhouse supplemented with artificial light for 16 h per day and watered as needed. All seedling pots were randomly placed in the greenhouse and reassigned randomly to new positions weekly. At the start of the experiment, seedlings of the same height and size of *S. canadensis* were planted in each plot to compete with weeds. Four common Chinese farmland weeds were utilized as competitive species:1) *Alternanthera philoxeroides*, 2) *Setaria viridis*, 3) *Digitaria sanguinalis*, and 4) *Amaranthus retroflexus*. Seedling of the same height and size of all four weed species were transplanted into each 3 × 2 m plot, with 60 cm deep cement border walls between plots, on July 1, 2011. To ensure that *S. canadensis* and weeds continued to compete, additional plants of the four weed species and *S. canadensis* were transplanted at the same time into each plot according to a fixed pattern that promoted interactions among the plants (Fig. S1b) again in July 2011. Each plot was planted with 12 *S. canadensis* plants (four plants each from three different populations of the same geographical cytotype [Table S1]), 6 *Alternanthera philoxeroides* plants, 12 *Setaria viridis* plants, 12 *Digitaria sanguinalis* plants and 12 *Amaranthus retroflexus* plants (Fig. S1b). Blank control (CK) plots were set up with the same number of weed plants minus *S. canadensis*. Transplanting was no longer required following the first year of the study as all transplanted subjects survived. Additionally, irrigation and fertilization were not used during the four years of the experiment.

Diploid plants of *S. canadensis* were totally outcompeted by competitive plant species by the sampling date in 2015. However, this supplanting process occurred gradually over the five growing seasons. Therefore, these plots were still considered as "diploids" within our data reporting. In the plots with native tetraploids plants, some *S. canadensis* plants had to be replaced, because of local extinction. The inflorescences of *S. canadensis* and the other weed plants were removed before seed maturation to prevent any seed dispersal into other plots.

2.3. Plant sampling and analyses

To minimize the influence of border effects, only plants of *S. canadensis* and weeds in the central area of each plot (4.8 m^2, 1.75 × 2.75 m) were sampled. Weed abundance was determined in the form of shoot dry matter in each plot in May 2015. The abundance and shoot dry matter of *S. canadensis* as well as each weeds species were determined again in November 2015. All plant samples were dried at 65 °C for at least 72 h and weighed to 0.001 g. Additional subsamples were taken from each dried sample for grinding before mineral nutrient analysis. Plant N concentration was measured with an Elementar Vario Marco Cube (Elementar, Hanau, Germany). The total shoot N content was calculated by multiplying the biomass by the N concentration. The biomass of weeds and *S. canadensis* in each plot was summed and presented in one Figure (Fig. 1).

2.4. Soil sampling and analyses

2.4.1. Soil sampling

Soil samples were collected in summer (July 18) and fall (November 9) of 2015 for chemical analyses. The soil had a pH (H_2O) of 8.0, and total C, N, P and K contents of 19.1, 1.66, 0.56 and 12.43 g kg^{-1} of soil, respectively. Four soil cores (3 cm diameter and 0–15 cm depth) were obtained across each plot at a minimum of 2 cm apart from *S. canadensis* and weed plants, samples were composited into one sample. Soil samples were sieved to < 2 mm and 20 g of each sample were immediately frozen for fatty acid analysis. Microbial and chemical analyses were carried out within seven days of sampling on the sieved soil stored at 4 °C.

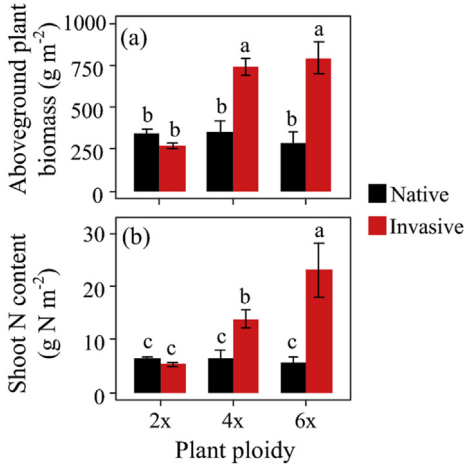

Fig. 1. Effects of *Solidago canadensis* ploidy (diploid: 2*x*, tetraploid: 4*x*, hexaploid: 6*x*) and origin (native: black; introduced/invasive: red) on aboveground plant biomass and shoot nitrogen (N) content in November. Different letters indicate significant differences among groups (Fisher's LSD test, $P < 0.05$). Error bars are standard errors of means ($n = 4$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.4.2. Soil analyses

Microbial respiration was measured as the carbon dioxide (CO_2) emitted during incubation for 8 h at 25 °C without any substrate addition (Hu and vanBruggen, 1997). Dissolved organic carbon (DOC) was extracted from fresh soil using ultrapure water. The filtrate that passed through a 0.45 mm filter membrane was analyzed with a total C analyzer (Elementar, Germany). Net mineralization and net nitrification were determined using the aerobic incubation procedure described by Hart et al. (1994). Net N mineralization was obtained using a 25 g subsample of moist soil from each field. Moist soil samples were incubated for 28 days at room temperature (approximately 25 °C) in a 250-ml specimen cup, covered with a perforated plastic cap to allow gas exchange while minimizing evaporation (Verchot et al., 2001). Ammonium N (NH_4^+-N) and nitrate N (NO_3^--N) were extracted using a 1:5 (m:v) soil: 2M KCl suspension and filtrated through paper. The N measurements were made to distinguish ammonium N (NH_4^+-N) and nitrate N (NO_3^--N) (Bremner and Keeney, 1966) on a continuous flow analyzer (Skalar, Holland).

2.4.3. Soil microbial community analysis

The composition of soil microbial communities was characterized using phospholipid fatty acids (PLFA) as described by Bossio et al. (1998) with slight modifications, using the gas chromatography conditions and nomenclature described by Buyer and Sasser (2012). Freeze-dried soils were extracted with 25 ml of a 1:2:0.8 (v:v:v) chloroform-methanol-citrated buffer mixture (25 ml in 50 ml falcon tube). The total lipid was separated into phospholipids, neutral lipids, and glycolipids using solid-phase extraction (SPE) tubes (ANPEL Laboratory Technologies Inc., China) containing 0.5 g anhydrous sodium sulfate. The phospholipids were trans-esterified by a mild alkaline methanolysis (Bossio et al., 1998) and the resulting fatty acid methyl esters were extracted into hexane and dried under N_2. Samples were redissolved into hexane and analyzed on an Agilent 6850 series Gas Chromatograph, using the MIDI peak identification software (version 4.5; MIDI Inc., Newark, DE). A known amount of the internal standard (IS), 1,2-dinonadecanoyl-sn-glycero-3-phosphocholine (19:0 PC, Avanti Polar Lipids p/n 850367), was added at the beginning of the process. The abundant PLFAs were ascribed to Gram-positive bacteria (i14:0, i15:0, a15:0, i16:0, i17:0 and a17:0), Gram-negative bacteria (16:1ω9c, cy17:0,18:1ω9c and cy19:0), saprotrophic fungi (18:2ω6c), arbuscular mycorrhizal fungi (AMF) (16:1ω5c), and actinobacteria (10Me16:0, 10Me17:0, 10Me18:0, and 10Me20:0) (Ruess and Chamberlain, 2010) (Table S8). The total and microbial group-specific PLFA were quantified as: Total PLFA (nmol/g) = (total PLFA peak area – 19:0 peak area) × n/19:0 (nmol/g) (n: method parameters). Microbial group (nmol/g) = Total PLFA (nmol/g) × Microbial group (%).

2.4.4. AMF root colonization and spore density in soil

Roots of *S. canadensis* collected in July were rinsed within 48 h of collection, and lateral fine roots (< 1 mm) sampled for analyses. The roots collected for analyses after clearing and staining according to Philips and Hayman (1970) with slight modifications. Briefly, the roots were cleared for 40 min in a 10% KOH solution at 90 °C, placed in a 1% HCl solution for 2 min and stained in a glycerol water–trypan blue solution (0.065% w/v) at 90 °C for 15 min. Root colonization by AMF was assessed at 45 × to 100 × magnification, using the gridline-intersect method (Giovannetti and Mosse, 1980). Spores density of AMF in soil was determined after wet sieving and density gradient centrifugation (Daniels and Skipper, 1982).

2.4.5. Free-living nematodes in soil

The nematode populations were extracted from 100 g fresh soil using a sequential extraction method (Liu et al., 2008). After the total number of nematodes was recorded, 100 specimens per sample were randomly selected and identified to the genus level. The minimum number of nematodes in any soil sample was 219. The nematodes were assigned to the following trophic guilds: bacterivores, fungivores, herbivores and omnivore-carnivores (Yeates et al., 1993).

2.5. Statistical analyses

Analysis of variance (ANOVA) and Fisher's least significant difference (LSD) tests were performed using Statistica version 7.1 (StatSoft Inc., Tulsa, OK, USA). Since the measurements were repeated on the same plot in summer and autumn, repeated measures ANOVA were used to test the effects of plant polyploidy (2*x*, 4*x*, 6*x*) and origin (introduced and native) on soil nutrients, soil microbial biomass and abundance of soil biota at July and November. The Adonis function in the 'vegan' package of R was used to perform a permutation multivariate analysis of variance (PERMANOVA). Statistical significance for the effect of polyploidy and origin were tested using permutation pseudo-*F* ratios.

3. Results

3.1. Plant and soil properties

Both ploidy and origin of *S. canadensis* both significantly affected above-ground plant biomass ($P < 0.001$, $F_{2,18} = 13.32$, Table S2). Above-ground plant biomass was significantly higher for invasive tetra- (745.51 ± 49.47 g m^2) and hexa-ploids (793.64 ± 94.69 g m^2) than their native counterparts (351.47 ± 71.99 g m^2 and 290.61 ± 60.91 g m^2, respectively) in November (Fig. 1a). The effect of origin and ploidy on shoot N content was dependent on plant origin, with only invasive polyploids having a higher biomass N ($P < 0.001$, $F_{2,18} = 8.38$, Table S2). Total shoot N was significantly higher for introduced tetra- and hexa-ploids than their native counterparts in November (Fig. 1b), as the N concentration was also higher in tetra- and hexa-ploids (13.43 ± 2.03 and 23.34 ± 7.94 mg g^{-1}) than in diploids (7.75 ± 0.60 mg g^{-1}%)($P < 0.001$, $F_{2,18} = 42.09$).

Dissolved organic C (Fig. 2a–b, $P < 0.001$, $F_{2,34} = 116.3$, Table S3) and soil microbial respiration (Fig. 2g and h, $P < 0.001$, $F_{2,34} = 143.5$, Table S3) were significantly higher for tetra- and hexa-ploids than diploids, independent of origin. Both ploidy and origin significantly affected soil nitrate nitrogen (NO_3^--N) ($P < 0.05$, $F_{2,34} = 27.4$, Fig. 2c-f, Table S3), but none of them had any significant effect on soil ammonium nitrogen (NH_4^+-N). For tetra- and hexa-ploids, soil nitrate

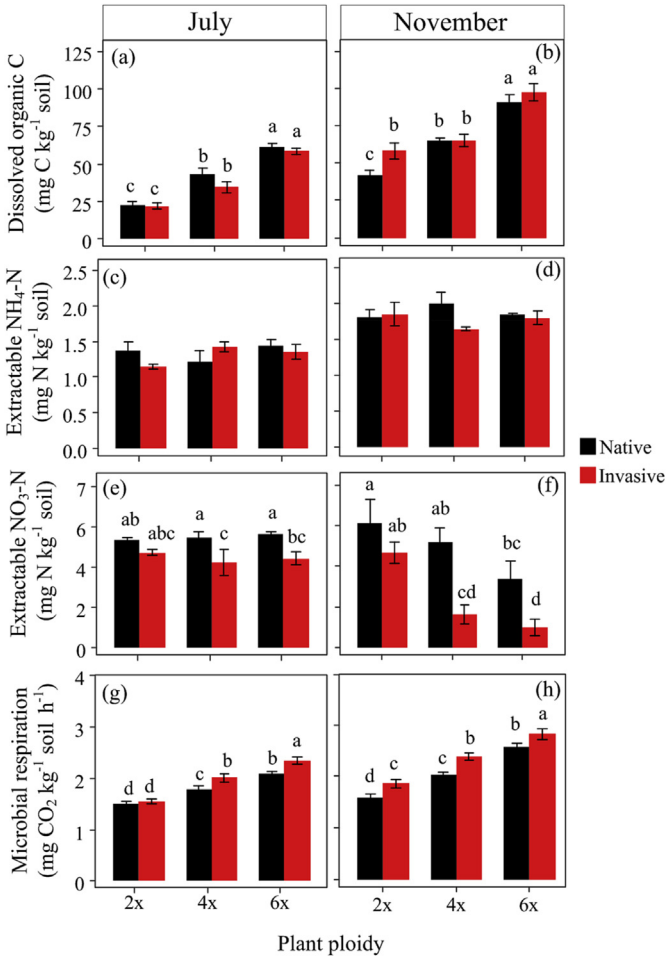

Fig. 2. Effects of *Solidago canadensis* ploidy (diploid: 2*x*, tetraploid: 4*x*, hexaploid: 6*x*) and origin (native: black; introduced/invasive: red) on dissolved organic carbon (a, b), extractable ammonium nitrogen (c, d), extractable nitrate nitrogen (e, f) in soil, and soil microbial respiration (g, h) in July and November. Different letters indicate significant differences among groups (Fisher's LSD test, $P < 0.05$). Error bars are standard errors of means ($n = 4$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

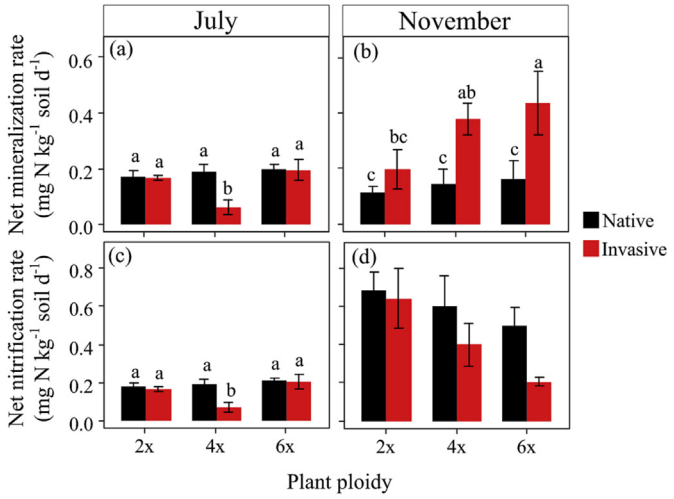

Fig. 3. Effects of *Solidago canadensis* ploidy (diploid: 2*x*, tetraploid: 4*x*, hexaploid: 6*x*) and origin (native: black; introduced/invasive: red) on net mineralization rate (a, b) and net nitrification rate (c, d) in July and November. Different letters indicate significant differences among groups (Fisher's LSD test, $P < 0.05$). Error bars are standard errors of means ($n = 4$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

nitrogen (NO_3^--N) was significantly lower under invasive than native counterparts both in July ($P < 0.01$, $F_{1,18} = 13.29$, Fig. 2e) and November ($P < 0.001$, $F_{1.18} = 16.67$, Fig. 2f). In the November, both the origin and polyploidy of *S. canadensis* affected NO_3–N (Fig. 2f, $P < 0.01$, $F_{2,18} = 7.94$). Also, net mineralization rate was significantly lower under tetra- and hexa-ploids than diploids in November (Fig. 3b, $P < 0.05$, $F_{2,18} = 4.29$).

3.2. Soil microbial biomass and community composition

Both the origin and polyploidy of *S. canadensis* significantly affected total microbial biomass ($P < 0.05$, $F_{2,34} = 4.53$, Fig. 4a and b, Table S4). Differing ploidy levels of *S. canadensis* also led to significant divergence in the composition and structure of the soil microbial community, particularly in November ($P < 0.01$, $F_{2,23} = 6.77$, Fig. 6b, Table S5). The biomass of arbuscular mycorrhizal fungal in soil was not significantly different among the *S. canadensis* plants of different origin and ploidy in July (Fig. 4c, $P = 0.162$, $F_{2,18} = 2.01$), but was significantly higher under invasive than native tetra- and hexa-ploids in November ($P < 0.001$, $F_{2,18} = 13.97$, Fig. 4d, Table S4). A similar trend was observed for the biomass of saprotrophic fungi, which were more abundant under invasive than native plants ($P < 0.001$, $F_{2,34} = 6.06$, Fig. 4e–f, Table S4). The biomass of Gram-positive bacteria was markedly higher under invasive tetra- and hexa-ploidy plants than native plants of the same ploidy ($P < 0.001$, $F_{2,34} = 8.17$, Fig. 4g-h, Table S4), while more Gram-negative bacteria were consistently associated with polyploids ($P < 0.001$, $F_{2.34} = 10.64$, Fig. 4i-j, Table S4). The biomass of actinomycetes were significantly higher under invasive tetra- and hexa-ploids than native plants of the same ploidy in both July ($P < 0.01$, $F_{2,18} = 13.34$, Fig. 4k) and November ($P < 0.01$, $F_{2,18} = 7.75$, Fig. 4l).

3.3. AMF root colonization and spore density in soil

Ploidy of *S. canadensis* influenced root colonization by AMF ($P < 0.05$, $F_{2,18} = 5.434$, Table S7, Fig. 7a), and this effect was higher in soil under tetra- and hexa-ploids than diploids in July. The origin of *S. canadensis* had no significant effect on root colonization by AMF ($P = 0.469$, $F_{2,18} = 0.546$, Table S7, Fig. 7a) or spore density ($P = 0.762$, $F_{2,18} = 0.095$, Table S7, Fig. 7b). Spore density in soil was, however, significantly lower under hexa-ploids than diploids in July ($P < 0.05$, $F_{2,18} = 6.028$, Table S7, Fig. 7b).

3.4. Free-living nematodes and herbivorous nematodes in soil

In general, the nematode numbers varied considerably among the experimental replicate plots, and both ploidy and origin of *S. canadensis* significantly affected them (Fig. 5). The ploidy levels of *S. canadensis* significantly affected the trophic structure of the free-living nematodes in soil in July ($P < 0.001$, $F_{2,23} = 4.60$, Fig. 6c, Table S5) and November ($P < 0.01$, $F_{2,23} = 3.09$, Fig. 6d, Table S5). Ploidy of *S. canadensis* influenced the abundance of bacterivores that was higher under invasive tetraploids than natives in November ($P < 0.01$, $F_{2,18} = 7.99$, Fig. 5b, Table S6). Ploidy of *S. canadensis* had no significant effect on fungivores, although they tended to increase in November ($P = 0.153$, $F_{2,18} = 2.08$, Fig. 5d, Table S6).

The abundance of herbivorous nematodes was higher in soil under invasive than native hexa-ploids in November ($P < 0.001$, $F_{2,18} = 21.14$, Fig. 5f, Table S6). Under invasive *S. canadensis*, omnivores + carnivores were more abundant under tetra- and hexa-ploids than diploids in July ($P < 0.05$, $F_{2,18} = 4.99$, Fig. 5g, Table S6), but the opposite trend emerged under native plants, although the difference

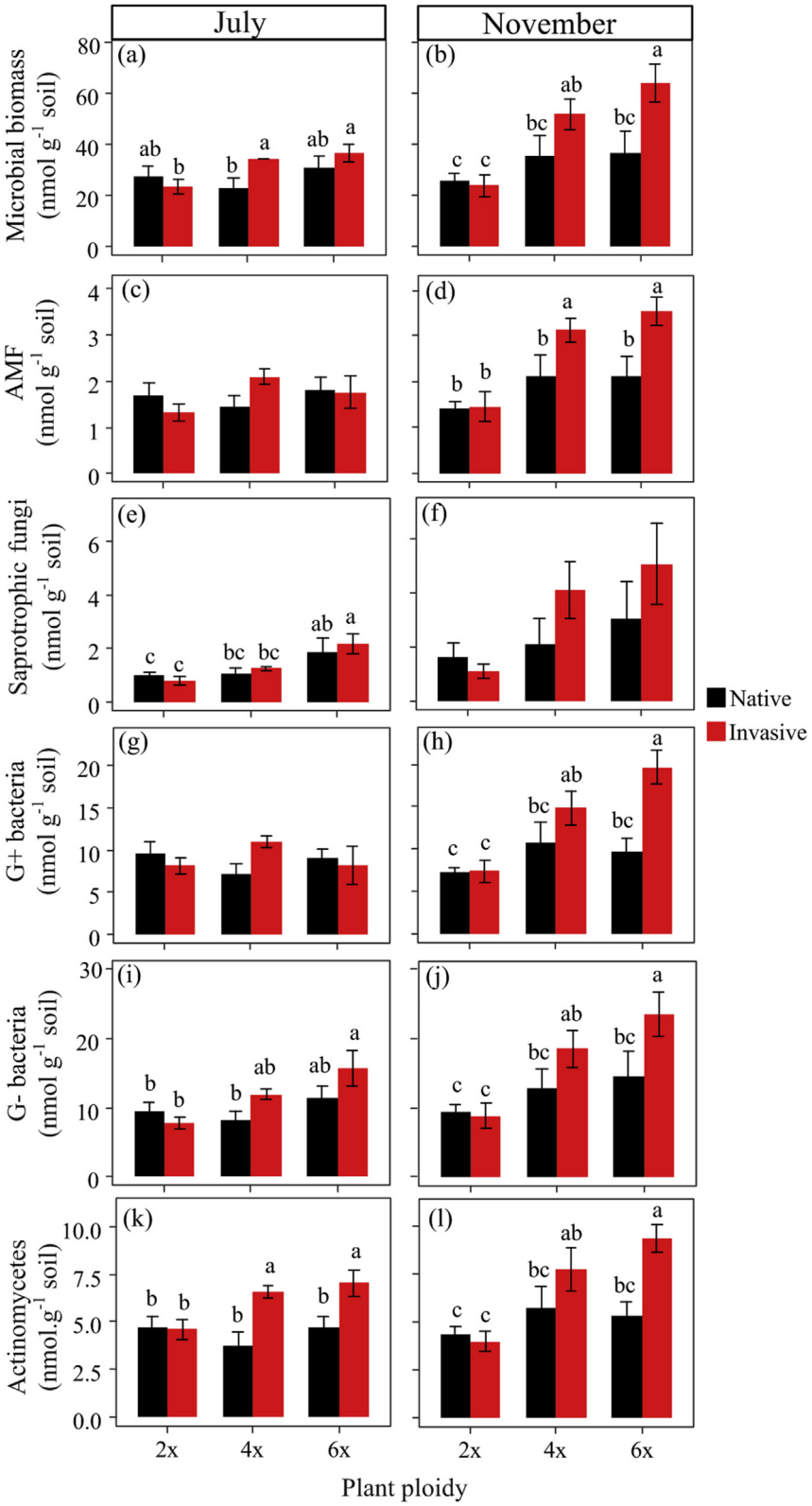

Fig. 4. Effects of *Solidago canadensis* ploidy (diploid: 2*x*, tetraploid: 4*x*, hexaploid: 6*x*) and origin (native: black; introduced/invasive: red) on the biomass of the overall microbial community (a, b), arbuscular mycorrhizal fungi(AMF) (c, d), saprophytic fungi (e, f), Gram-positive (G^+) bacteria (g, h), Gram-negative (G^-) bacteria (i, j), and actinomycetes (k, l) in July and November. Different letters indicate significant differences among groups (Fisher's LSD test, $P < 0.05$). Error bars are standard errors of mean ($n = 4$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

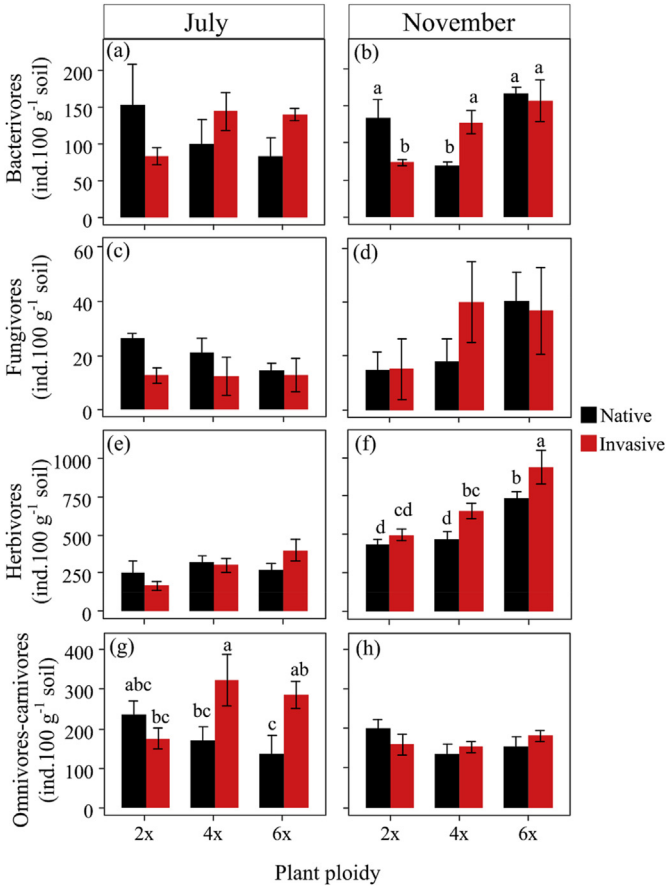

Fig. 5. Effects of *Solidago canadensis* ploidy (diploid: 2*x*, tetraploid: 4*x*, hexaploid: 6*x*) and origin (native: black; introduced/invasive: red) on the number of bacteria-feeding nematodes (a, b), fungi-feeding nematodes (c, d), plant-feeding nematodes (e, f), and omnivores + carnivores (g, h) in July and November. Different letters indicate significant differences among groups (Fisher's LSD test, $P < 0.05$). Error bars are standard errors of means ($n = 4$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

was not statistically significant.

4. Discussion

Both 'ploidy' and 'origin' of *S. canadensis* significantly affected plant biomass and N uptake (Fig. 1a and b), as well as soil microbes and nematodes (Figs. 4 and 5). However, 'ploidy' played a dominant role as it explained most of variance among the different treatments. The magnitude of differences in microbes and nematodes often corresponded with a difference in plant biomass, suggesting a bottom-up control by plants via altered organic C inputs.

4.1. Microbes and nematodes in soil under tetra- and hexa-ploids enhance soil nutrient cycling

Our common garden experiment showed that tetra- and hexa-ploidy plants of *S. canadensis* take up significantly more N (Fig. 1b), produced more DOC (Fig. 2a and b), supported a larger microbial biomass (Fig. 4a and b) and promoted higher microbial respiration (Fig. 2g and h) in soil than diploid *S. canadensis* in the invasive range. Previous studies have shown increased gene expression in polyploid plants, along with enhanced root biomass (Kim et al., 2004; Kulkarni and Borse, 2010) and root secretion (Norby and Cotrufo, 1998; Jesus-Gonzalez and Weathers, 2003; Kim et al., 2004; Kulkarni and Borse, 2010). Thus, it is likely that differences in microbial abundance and activity under *S. canadensis* of different ploidy may explain dissimilarities in soil N availability and total plant N uptake. High microbial biomass and increased biological activities often increase nutrient availability to plants through enhancing microbial biomass turnover and mineralization (Zaman et al., 1999; Tu et al., 2003; Wang et al., 2004). We observed that high soil microbial biomass and activity were associated with high plant N uptake and lower soil N levels particularly under introduced tetra- and hexa-ploid *S. canadensis* (Fig. 1b, Table S2, Fig. 2f, Table S3). In addition, soil bacteria and fungi, as well as bacterivore and fungivore nematodes, tended to be more abundant under tetra- and hexa-ploid than diploid *S. canadensis* (Fig. 5a – d, Table S6). Soil microbes are generally C-limited and the higher C inputs under polyploid *S. canadensis* provide more food sources for bacteria and fungi (Wardle et al., 1999; Tu et al., 2003; Stephan et al., 2005). Bacteria and fungi are the prey of bacterivorous and fungivorous nematodes. Bacterial-feeding by nematodes is a mechanism by which microbial biomass N becomes plant available (Beare et al., 1992), also known as the microbial loop (Bonkowski, 2004). Moreover, bacterivorous nematodes may increase the mineralization of recalcitrant organic N (Zhu et al., 2018). Consequently, high root biomass and root exudation under tetra- and hexa-ploid *S. canadensis* may lead to a positive feedback between bacterivorous nematodes and invasive *S. canadensis* plants.

4.2. Effects of S. canandensis ploidy on arbuscular mycorrhizal fungi

The significantly higher AMF colonization of roots of hexa-ploid plants (Table S7, Fig. 7a), and soil AMF biomass (Table S4, Fig. 4c and d) suggest that polyploid *S. canadensis* may form stronger symbiotic ties with AMF. This finding is corroborated by those of a recent meta-analysis reporting that invasive plants often have higher AMF root colonization or support greater extraradical AMF abundance (Zhang et al., 2019). Zhang et al. (2010) found that invasive *S. canadensis* generated positive feedbacks by altering the AMF community composition; supporting AMF taxa that are favorable for its own, while reducing AMF taxa beneficial to native plants. Positive AMF effects on *S. canadensis* have also been documented in other studies (Jin et al., 2004; Sun and He, 2010). The change to AMF community structure was further found to reduce the competitiveness of a native plant (*Kummerowia striata*) (Zhang et al., 2010). Moreover, despite the generally low specificity in mycorrhizal symbiosis, the C allocated to each fungus for mycelial biomass can differ greatly depending on their exploration strategy (Agerer, 2001), nutrient mobilization ability (Talbot et al., 2015), and host symbiotic preferences. Pérez-Izquierdo et al. (2019) suggested that the plant genotype may select for fungal clades with diverse abilities; thus, influencing the phylogenetic community structure through competition. As AMF can effectively transfer N from the soil to plant roots (Govindarajulu et al., 2005), the increased AMF colonization of roots and higher AMF biomass in soil may have contributed to the heightened N uptake of tetra- and hexaploids (Table S2, Fig. 1) in addition to root exploration of soil N (Table S3, Fig. 2e and f). Together, our results suggest that higher AMF could thus contribute to increased N uptake by invasive polyploid *S. canadensis*, promoting N mineralization.

4.3. Increased abundances of herbivorous nematodes under tetra- and hexaploid S. canadensis

Our experiment revealed the effect of polyploidy on nematode abundance to be trophic group specific. While the number of bacterivores and omnivores + carnivores did not differ depending on the ploidy of *S. canadensis*, the amount of fungivores and herbivores were greater under polyploids (Fig. 5c–f, Table S6). The influence of polyploidy on herbivores may vary according to cytotype (Hull-Sanders et al., 2009). Tetra- and hexa-ploid *S. canadensis* may provide a better advantage to microbes and plant-feeding nematodes compared to diploids due to their increased mineral nutrient uptake (Mattson, 1980). The success of plant invasion in new ranges has often been attributed to

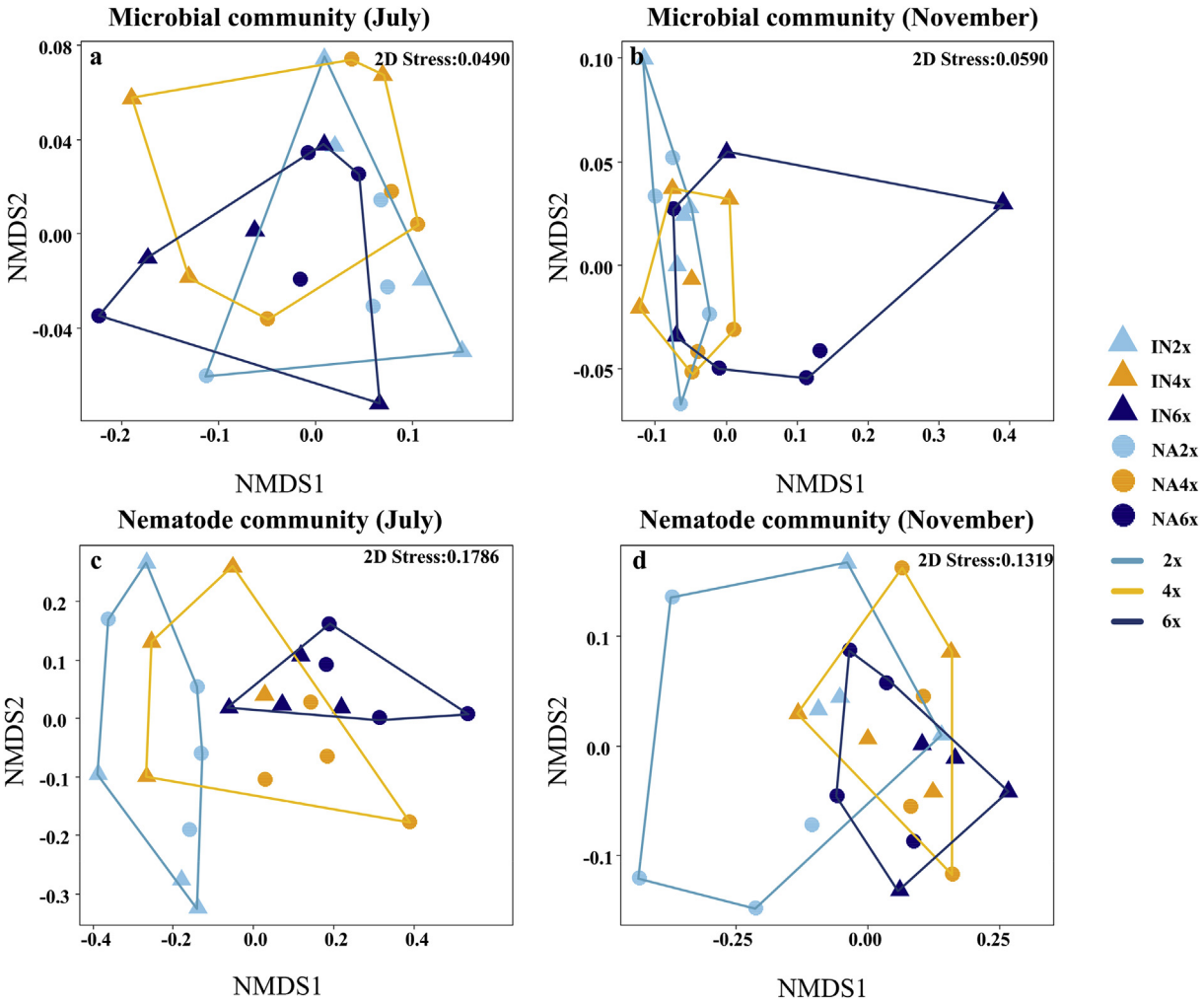

Fig. 6. Nonmetric multidimensional scaling (NMDS) plot showing the dissimilarity of microbial community structure (a, b) and nematode community structure (c, d) between genotypes of *Solidago canadensis* differing in ploidy in July and November. IN, introduced/invasive; NA, native; 2*x*, diploid; 4*x*, tetraploid; 6*x*, hexaploid.

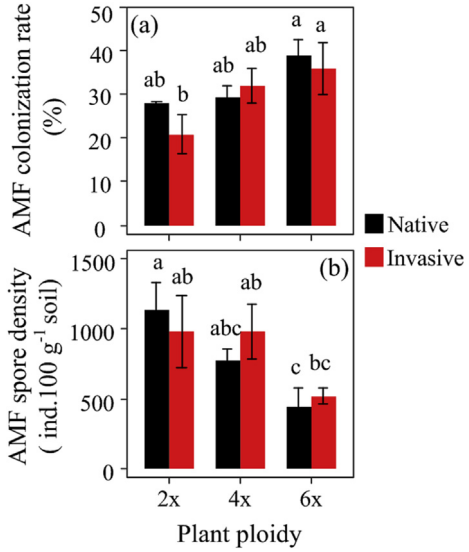

Fig. 7. Effects of Solidago *canadensis* ploidy (diploid: 2*x*, tetraploid: 4*x*, hexaploid: 6*x*) and origin (native: black; introduced/invasive: red) on arbuscular mycorrhizal fungal (AMF) colonization rate of root (a) and spore density in soil (b). Different letters indicate significant differences among groups (Fisher's LSD test, $P < 0.05$). Error bars are standard errors of means ($n = 4$).

"natural enemy" release within that newly invaded region (Mack et al., 2000; Keane and Crawley, 2002; Mitchell and Power, 2003). However, natural enemies such as herbivores may accumulate over time, gradually impairing invasive plants (Siemann et al., 2006; Diez et al., 2010). While at the same time gradually divesting energy towards mechanisms that promote defense against pathogens and herbivores due to their seemingly low threat (Blossey and Notzold, 1995). The observed accumulation of root-feeding nematodes under tetra- and hexa-ploid *S. canadensis* without negatively affecting plant growth was surprising. Further research is required regarding the intricacies of plant polyploidy and plant-parasitic nematode interactions in a newly introduced range.

4.4. The impact of S. canadensis origins on soil microbes and nematodes

The origin of *S. canadensis* also had a significant effect as soil microbes and nematodes were higher under invasive than native *S. canadensis* (Figs. 4 and 5). This effect was likely related to the difference in plant C sources allocated belowground. Although root biomass was specifically measured in our study, the shoot biomass of invasive polyploids was twice more than their native counterparts (Fig. 1a). *S. canadensis* is a rhizome plant that allocates high proportion of photosynthates belowground. Invasive plants generally produce more C resources than natives (Ehrenfeld, 2003; Liao et al., 2008), increasing both litter and labile C (e.g. root exudates) inputs (Ehrenfeld, 2003; Liao et al., 2008; Prescott and Zukswert, 2016; Zhang et al., 2019).

Zhang et al. (2009) found that soil microbial biomass, activity, and functional diversity significantly increased with *S. canadensis* invasion in China. High AMF colonization of roots and AMF biomass observed in our study and other studies (Jin et al., 2004; Sun and He, 2010) also provide indirect evidence of increased C inputs belowground. Higher C inputs under invasive plants likely elicit a positive feedback loop in which plants increase microbial biomass and activities, and thus enhance microbe feeders and nutrient release, feeding back to plant growth (Bonkowski, 2004; Van der Putten et al., 2007; Meisner et al., 2011; Zhang et al., 2019).

Our findings suggest that plant polyploidization may have a cascading effect on soil food webs, affecting horizontal (competitive) and vertical (consumer-resource) interactions (Guignard et al., 2017). Polyploidy provided additional C resources in the form of root exudates and dead roots for soil microbes, and supported higher inter-trophic microbial predators which promoted nutrient turnover, positively feeding back to invasive *S. canadensis*. Soil nutrients (i.e. N and P) can also influence the performance of plants of differing ploidy; unlike diploids, when nutrients are in excess, polyploid plants tend to increase in biomass production and competitiveness. This is one reason why many crops such as wheat and cotton are polyploids (Leitch and Leitch, 2008). High inputs of chemical nutrients (N fertilizers in particular) often have negative effects on the environment (Galloway et al., 2008). Nutrient use efficiency (NUE) in polyploid crops may be improved by selecting morphological and physiological traits of roots that maximize nutrient uptake (Richardson et al., 2011), which would not only increase N use efficiency and economic profits (Kant et al., 2011), but also reduce environmental costs.

In summary, we recorded that origin and ploidy of *S. canadensis* influenced soil chemical and microbial properties. Soil microbial biomass and activities, and AMF abundance were higher, but soil extractable N was lower under tetra- and hexa-ploid than diploid *S. canadensis*. In general, the biomass of all microbial groups were higher in soil under introduced populations of tetra- and hexa-ploids than under native populations of tetra- and hexa-ploids. Bacterivores and omnivore + carnivores were not significantly affected, but fungi-feeding and root-feeding nematodes tended to be more abundant under tetra- and hexa-ploids than diploids. These results suggest that the competitive advantage of tetra- and hexa-ploid over diploid *S. canadensis* may be due to stimulation of microbial N turnover for increased N uptake.

Our study also presented four crucial aspects that should be taken into consideration by future researchers: 1) the common garden experiment was conducted only at one single location, the potential effects of different soil and climatic conditions on *S. canadensis* were not considered, but may be significant in the spread and growth of *S. canadensis* (Petrů and Tielbörger, 2008); 2) the physical and chemical properties and nutrient availability (Vanderhoeven et al., 2005; Stefanowicz et al., 2017) in soil may also affect the growth of *S. canadensis* and interactions with soil microbes (Oldroyd, 2013); 3) neighboring plants of differing biological mechanisms may have influenced the microbial communities and nutrient dynamics (Chagnon et al., 2019); and 4) the PLFA method has low resolution and combination of high-throughput sequencing with PLFA would have provided a better resolution. Future studies should investigate possible negative feedback loops by root-feeding nematodes on polyploid performance, while also mitigating effects by site differences, such as soil, climate and accompanying biota.

Acknowledgements

This study was supported by the National Natural Science Foundation of China (grant numbers 41877057 and 41571244). We thank professor Shuijin Hu (North Carolina State University) for his insightful comments that greatly improved the manuscript. We thank Miss Jingxuan Xu and Mr. Zhengkun Hu, Xianghong Yang for their help with sampling, measurements and data analysis. The authors declare no competing financial interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2019.107594.

References

Agerer, R., 2001. Exploration types of ectomycorrhizae. Mycorrhiza 11, 107–114.
Augspurger, C.K., Kelly, C.K., 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61, 211–217.
Beare, M.H., Parmelee, R.W., Hendrix, P.F., Cheng, W., Coleman, D.C., Crossley Jr., D.A., 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecological Monographs 62, 569–591.
Bever, J.D., 2002. Negative feedback within a mutualism: host–specific growth of mycorrhizal fungi reduces plant benefit. Proceedings of the Royal Society of London. Series B: Biological Sciences 269, 2595–2601.
Bever, J.D., 2003. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. New Phytologist 157, 465–473.
Bever, J.D., Westover, K.M., Antonovics, J., 1997. Incorporating the soil community into plant population dynamics: the utility of the feedback approach. Journal of Ecology 85, 561–573.
Birchler, J.A., 2012. Polyploidy and Genome Evolution. Springer, Berlin.
Blossey, B., Notzold, R., 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83, 887–889.
Bonkowski, M., 2004. Protozoa and plant growth: the microbial loop in soil revisited. New Phytologist 162, 617–631.
Bossio, D.A., Scow, K.M., Gunapala, N., Graham, K.J., 1998. Determinants of soil microbial communities: effects of agricultural management, season, and soil type on phospholipid fatty acid profiles. Microbial Ecology 36, 1–12.
Bradford, M.A., Strickland, M.S., DeVore, J.L., Maerz, J.C., 2012. Root carbon flow from an invasive plant to belowground foodwebs. Plant and Soil 359, 233–244.
Bremner, J.M., Keeney, D.R., 1966. Determination and isotope-ratio analysis of different forms of nitrogen in soils: 3. exchangeable ammonium, nitrate, and nitrite by extraction-distillation methods 1. Soil Science Society of America Journal 30, 577–582.
Buyer, J.S., Sasser, M., 2012. High throughput phospholipid fatty acid analysis of soils. Applied Soil Ecology 61, 127–130.
Callaway, R.M., Thelen, G.C., Rodriguez, A., Holben, W.E., 2004. Soil biota and exotic plant invasion. Nature 427, 731–733.
Callaway, R.M., Cipollini, D., Barto, K., Thelen, G.C., Hallett, S.G., Prati, D., Klironomos, J., 2008. Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89, 1043–1055.
Chagnon, P.L., Bradley, R.L., Klironomos, J.N., 2019. Mycorrhizal network assembly in a community context: the presence of neighbours matters. Journal of Ecology 00, 1–12. https://doi.org/10.1111/1365-2745.13230.
Colautti, R.I., Grigorovich, I.A., MacIsaac, H.J., 2006. Propagule pressure: a null model for biological invasions. Biological Invasions 8, 1023–1037.
Daehler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annual Review of Ecology, Evolution, and Systematics 34, 183–211.
Daniels, B.A., Skipper, H.A., Schenck, N.C., 1982. Methods and principles of mycorrhizal research. Soil Science 134, 405.
De Jesus-Gonzalez, L., Weathers, P.J., 2003. Tetraploid *Artemisia* annua hairy roots produce more artemisinin than diploids. Plant Cell Reports 21, 809–813.
Diez, J.M., Dickie, I., Edwards, G., Hulme, P.E., Sullivan, J.J., Duncan, R.P., 2010. Negative soil feedbacks accumulate over time for non native plant species. Ecology Letters 13, 803–809.
Ehrenfeld, J.G., 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6, 503–523.
Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P., Sutton, M.A., 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 32, 889–892.
Giovannetti, M., Mosse, B., 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytologist 84, 489–500.
Goldberg, D.E., Landa, K., 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. Journal of Ecology 79, 1013–1030.
Govindarajulu, M., Pfeffer, P.E., Jin, H., Abubaker, J., Douds, D.D., Allen, J.W., Shachar-Hill, Y., 2005. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. Nature 435, 819–823.
Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111, 1169–1194.
Guignard, M.S., Leitch, A.R., Acquisti, C., Eizaguirre, C., Elser, J.J., Hessen, D.O., Jeyasingh, P.D., Neiman, M., Richardson, A.E., Soltis, P.S., Soltis, D.E., Stevens, C.J., Trimmer, M., Weider, L.J., Woodward, G., Leitch, I.J., 2017. Impacts of nitrogen and phosphorus: from genomes to natural ecosystems and agriculture. Frontiers in Ecology and Evolution 5, 70–79.
Hart, S.C., Stark, J.M., Davidson, E.A., Firestone, M.K., 1994. In: Page, A.L., Miller, R.H., Kenney, D.R. (Eds.), Methods of Soil Analysis, Part 2. Microbiological and Biochemical Properties. Soil Science Society of America, Madison, Wisconsin, USA, pp. 985–1017.

Hierro, J.L., Maron, J.L., Callaway, R.M., 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. Journal of Ecology 93, 5–15.
Hodáňová, D., 1981. Plant strategies and vegetation processes. Biologia Plantarum 23 254-254.
Hu, S., vanBruggen, A.H.C., 1997. Microbial dynamics associated with multiphasic decomposition of ^{14}C-labeled cellulose in soil. Microbial Ecology 33, 134–143.
Hull-Sanders, H.M., Johnson, R.H., Owen, H.A., Meyer, G.A., 2009. Influence of polyploidy on insect herbivores of native and invasive genotypes of *Solidago gigantea* (Asteraceae). Plant Signaling & Behavior 4, 893–895.
Jin, L., Gu, Y., Xiao, M., Chen, J., Li, B., 2004. The history of *Solidago canadensis* invasion and the development of its mycorrhizal associations in newly-reclaimed land. Functional Plant Biology 3110, 979–986.
Kant, S., Bi, Y.M., Rothstein, S.J., 2011. Understanding plant response to nitrogen limitation for the improvement of crop nitrogen use efficiency. Journal of Experimental Botany 62 1499-1509.
Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17, 164–170.
Keddy, P., Fraser, L.H., Wisheu, I.C., 1998. A comparative approach to examine competitive response of 48 wetland plant species. Journal of Vegetation Science 9, 777–786.
Kim, Y.S., Hahn, E.J., Murthy, H.N., Paek, K.Y., 2004. Effect of polyploidy induction on biomass and ginsenoside accumulations in adventitious roots of ginseng. Journal of Plant Biology 47, 356–360.
Kulkarni, M., Borse, T., 2010. Induced polyploidy with gigas expression for root traits in *Capsicum annuum* (L.). Plant Breeding 129, 461–464.
Leitch, A.R., Leitch, I.J., 2008. Genomic plasticity and the diversity of polyploid plants. Science 320, 481–483.
Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., Chen, J.K., Li, B., 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytologist 2008 706–714.
Liu, M., Chen, X., Qin, J., Wang, D., Griffiths, B., Hu, F., 2008. A sequential extraction procedure reveals that water management affects soil nematode communities in paddy fields. Applied Soil Ecology 40, 250–259.
Lopez-Zamora, I., Comerford, N.B., Muchovej, R.M., 2004. Root development and competitive ability of the invasive species *Melaleuca quinquenervia(cav.) S.T. blake* in the south Florida flatwoods. Plant and Soil 263, 239–247.
Lu, J., Weng, E., Wu, X., Weber, E., Zhao, B., Li, B., 2007. Potential distribution of *Solidago canadensis* in China. Acta Phytotaxonomica Sinica 45, 670–674.
Mack, R.N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10, 689–710.
Marchant, D.B., Soltis, D.E., Soltis, P.S., 2005. Genome evolution in plants. Plant Molecular Biology 42, 225–249.
Mattson Jr., W.J., 1980. Herbivory in relation to plant nitrogen content. Annual Review of Rcology and Systematics 11, 119–161.
Meisner, A., de Boer, W., Verhoeven, K.J., Boschker, H.T., van der Putten, W.H., 2011. Comparison of nutrient acquisition in exotic plant species and congeneric natives. Journal of Ecology 99, 1308–1315.
Mitchell, C.E., Power, A.G., 2003. Release of invasive plants from fungal and viral pathogens. Nature 421, 625–627.
Nash, S.K., Goldberg, D.E., Hartman, K.M., 2003. Relationships among species traits: separating levels of response and identifying linkages to abundance. Ecology 84, 1–16.
Norby, R.J., Cotrufo, M.F., 1998. Global change: a question of litter quality. Nature 396, 17–18.
Oldroyd, G.E., 2013. Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. Nature Reviews Microbiology 11, 252–263.
Parker, M.A., 2001. Mutualism as a constraint on invasion success for legumes and rhizobia. Diversity and Distributions 7, 125–136.
Pérez-Izquierdo, L., Zabal-Aguirre, M., González-Martínez, S.C., Buée, M., Verdú, M., Rincón, A., Goberna, M., 2019. Plant intraspecific variation modulates nutrient cycling through its belowground rhizospheric microbiome. Journal of Ecology 107, 1594–1605.
Petrů, M., Tielbörger, K., 2008. Germination behaviour of annual plants under changing climatic conditions: separating local and regional environmental effects. Oecologia 155, 717–728.
Phillips, J.M., Hayman, D.S., 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Transactions of the British Mycological Society 55, 158–161.
Pimentel, D., Lach, L., Zuniga, R., Morrison, D., 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50, 53–66.
Prescott, C.E., Zukswert, J.M., 2016. Invasive plant species and litter decomposition: time to challenge assumptions. New Phytologist 209, 5–7.
Pyšek, P., Richardson, D.M., 2008. Traits associated with invasiveness in alien plants: where do we stand? In: Caldwell, M.M., Marburg, G.H., Durham, R.B.J., Würzburg, O.L.L., Stanford, H.A.M., Jena, E.D.S., Kiel, U.S. (Eds.), Biological Invasions. Springer, Berlin, pp. 97–122.
Ranney, T.G., 2006. Polyploidy: from evolution to new plant development. In: Combined Proceedings International Plant Propagators' Society, vol. 56. pp. 137–142.
Reinhart, K.O., Callaway, R.M., 2006. Soil biota and invasive plants. New Phytologist 170, 445–457.
Richardson, A.E., Lynch, J.P., Ryan, P.R., Delhaize, E., Smith, F.A., Smith, S.E., Harvey, P.R., Ryan, M.H., Veneklaas, E.J., Lambers, H., Oberson, A., Culvenor, R.A., Simpson, R.J., 2011. Plant and microbial strategies to improve the phosphorus efficiency of agriculture. Plant and Soil 349, 121–156.
Ruess, L., Chamberlain, P.M., 2010. The fat that matters: soil food web analysis using fatty acids and their carbon stable isotope signature. Soil Biology and Biochemistry 42, 1898–1910.
Siemann, E., Rogers, W.E., Dewalt, S.J., 2006. Rapid adaptation of insect herbivores to an invasive plant. Proceedings of the Royal Society B: Biological Sciences 273, 2763–2769.
Silvertown, J., 2004. Plant coexistence and the niche. Trends in Ecology & Evolution 19, 605–611.
Stefanowicz, A.M., Stanek, M., Nobis, M., Zubek, S., 2017. Few effects of invasive plants *Reynoutria japonica, Rudbeckia laciniata* and *Solidago gigantea* on soil physical and chemical properties. The Science of the Total Environment 574, 938–946.
Stephan, H., Alexei, V.T., Stefan, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 36, 191–218.
Sun, Z.K., He, W.M., 2010. Evidence for enhanced mutualism hypothesis: *Solidago canadensis* plants from regular soils perform better. PLoS One 5, e15418.
Talbot, J.M., Martin, F., Kohler, A., Henrissat, B., Peay, K.G., 2015. Functional guild classification predicts the enzymatic role of fungi in litter and soil biogeochemistry. Soil Biology and Biochemistry 88, 441–456.
Thébault, A., Gillet, F., Müller-Schärer, H., Buttler, A., 2011. Polyploidy and invasion success: trait trade-offs in native and introduced cytotypes of two Asteraceae species. Plant Ecology 212, 315–325.
Tu, C., Koenning, S.R., Hu, S., 2003. Root-parasitic nematodes enhance soil microbial activities and nitrogen mineralization. Microbial Ecology 46, 134–144.
Tyser, R.W., Key, C.W., 1988. Spotted knapweed in a natural area fescue grassland: an ecological assessment. Northwest Science 62, 151–160.
Van der Putten, W.H., Klironomos, J.N., Wardle, D.A., 2007. Microbial ecology of biological invasions. The ISME Journal 1, 28–37.
Van Kleunen, M., Schmid, B., 2003. No evidence for an evolutionary increased competitive ability in an invasive plant. Ecology 84, 2816–2823.
Vanderhoeven, S., Dassonville, N., Meerts, P., 2005. Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. Plant and Soil 275, 169–179.
Verchot, L.V., Holmes, Z., Mulon, L., Groffman, P.M., Lovett, G.M., 2001. Gross versus net rates of N mineralization and nitrification as indicators of functional differences between forest types. Soil Biology and Biochemistry 33, 1889–1901.
Wagenitz, G., 1964. *Solidago L.* Illustrierte flora von Mitteleuropa, vol. 6. pp. 16–29.
Wang, W.J., Smith, C.J., Chen, D., 2004. Predicting soil nitrogen mineralization dynamics with a modified double exponential model. Soil Science Society of America Journal 68, 1256–1265.
Wardle, D.A., 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biological Reviews 67, 321–358.
Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Ghani, A., 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. Ecological Monographs 69, 535–568.
Weber, E., 2017. Invasive Plant Species of the World: a Reference Guide to Environmental Weeds. Secend edition, CABI, Boston.
Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199, 213–227.
Yeates, G.W., Bongers, T., De Goede, R.G., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera - an outline for soil ecologists. Journal of Nematology 25, 315–331.
Zaman, M., Di, H.J., Cameron, K.C., 1999. A field study of gross rates of N mineralization and nitrification and their relationships to microbial biomass and enzyme activities in soils treated with dairy effluent and ammonium fertilizer. Soil Use & Management 15, 188–194.
Zhang, C.B., Wang, J., Qian, B.Y., Li, W.H., 2009. Effects of the invader *Solidago canadensis* on soil properties. Applied Soil Ecology 43, 163–169.
Zhang, Q., Yang, R., Tang, J., Yang, H., Hu, S., Chen, X., 2010. Positive feedback between mycorrhizal fungi and plants influences plant invasion success and resistance to invasion. PLoS One 5, e12380.
Zhang, P., Li, B., Wu, J., Hu, S., 2019. Invasive plants differentially affect soil biota through litter and rhizosphere pathways: a meta-analysis. Ecology Letters 22, 200–210.
Zhu, T., Yang, C., Wang, J., Zeng, S., Liu, M., Yang, J., Müller, C., 2018. Bacterivore nematodes stimulate soil gross N transformation rates depending on their species. Biology and Fertility of Soils 54, 107–118.