

Original Research

Effects of *Solidago canadensis* Invasion and Climate Warming on Soil Net N Mineralization

Guangqian Ren¹, Min He¹, Guanlin Li¹, A. Anandkumar¹, Zhicong Dai^{1,2},
Chris B Zou³, Zhiyuan Hu¹, Qiong Ran^{1,4}, Daolin Du^{1,2*}

¹Institute of Environment and Ecology, Academy of Environmental Health and Ecological Security, School of the Environment and Safety Engineering, Jiangsu University, Zhenjiang, China

²Institute of Agricultural Engineering, Jiangsu University, Zhenjiang, China

³Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, USA

⁴School of Management, Chongqing University of Technology, Chongqing 400054, China

Received: 29 September 2019

Accepted: 14 November 2019

Abstract

The rapid expansion of *Solidago canadensis* and climate warming in southeastern China may interactively affect soil net nitrogen (N) mineralization, which may lead to plant invasion. A greenhouse simulated experiment was conducted with invasion, warming, and their interaction to investigate these changes' effects on soil net N mineralization in an ecological system. Our results indicated that the average rate of net mineralization, nitrification, and ammonification decreased with invasion, warming, and their interaction. The enzyme activities and pH showed more sensitivity in warming than invasion, and have a similar decreased trend with net N mineralization response to environmental changes, except sucrase. At the same time, enzyme and pH may play a key role in the process of net N mineralization from Pearson's correlation and redundancy analysis, especially for sucrase and urease. In addition, the lower produced of litter biomass by plants growing in pots was also an important reason for the decrease of net N mineralization rate. These results indicated that the significant decrease in substrate quality (N availability) by the increase in invasion and warming may cause the deterioration of species production in soil, which will have important consequences for soil ecology, N-cycles, and plant invasion.

Keywords: climate warming, enzyme activity, net nitrogen mineralization, plant invasion, *Solidago canadensis*

Introduction

Mean global temperature has increased by approximately 0.74°C over the last century (1906-2005), and the global climatic models are predicted to raise the mean global temperature by 1.0 to 3.5°C in the next 50 to 100 years due to the joint influence of both natural and human factors [1]. In 2007 the IPCC indicated the reliability that human activities will lead to climate warming at 90%. The impact of human activities on climate warming mainly comprises emissions of greenhouse gases, changing properties of underlying surface, and releasing heat to the atmosphere [2]. This warming effect has resulted in reducing the temporal stability of plant community biomass production [3], altering the soil characteristics, and may lead to increased plant invasions [4]. Plant invasion is recognized as a species that is established outside of its natural past or present distribution [5] and believed to cause damage to the environment and human health [6]. On whose introduction and/or invasion may alter ecosystem properties and community dynamics, even participating in feedback loops that affect climate change [7]. For example, Yuan et al. [8] observed that exotic *Spartina alterniflora* invasion alters the ecosystem atmosphere exchange of CH₄, N₂O, and C sequestration in a coastal salt marsh in China. In addition, changes in an environment could significantly interact with other global change processes, such as biological invasions [9]. The previous study found that climate warming and biological invasion both can affect the nitrogen (N) cycle and content in soil [4, 10]. However, the potential for the warming and plant invasion interact in regulating soil N dynamics in the ecosystem has not been well studied.

Soil N plays an important role in impacting soil capacity to maintain biological productivity and regulating atmospheric N compositions [11]. The dynamic of N in soil will alter temporal-spatial distribution and performance of native plants, and even affect invasive plants through enhanced species invasiveness and community invisibility [12, 13]. In turn, the production of differing quantities and qualities of above- and below-ground biomass [14] with associated changes in competitive balance in favor of fast-growing invasive species and litter decomposition [15] may alter the N pools, forms, turnover and cycling in plant biomass, litter, and soil [15, 16]. Most studies focus on the N deposition effects on plant invasion, but the effect of plant invasion on the soil N dynamic is less known, especially for the net N mineralization, which occurs when inorganic N is released from litter and soil organic matter during decomposition [17] and is positively correlated with plant growth and litter production [18].

S. canadensis: A widespread notorious rhizomatous clonal weed native to North America [19] and introduced as a horticultural plant in 1913 that has become one of the most aggressive invasive perennial species in China,

invading abandoned fields, disturbed habitats, and farmland [20]. *S. canadensis* clonal growth can lead to a dense population that results in crowding out native vegetation [21, 22], causing severe damage to local biodiversity and the natural ecosystem. Furthermore, extracts from the rhizome of *S. canadensis* inhibited seed germination of wheat by at least 50% [23], seriously affecting agricultural production and food safety. Therefore, *S. canadensis* has been listed as one of the most destructive and widespread invasive plant species in China [24]. Although invasive *S. canadensis* has become a major concern around the world, processes contributing to soil N turnover from its invasion is still relatively unknown [25].

High N availability will increase native shrub canopy loss and mortality while favoring nonnatives, leading to higher biomass and cover of nonnative species [26]. However, though changes in environmental could significantly interact with biological invasions [9], few explicit experiments have been conducted to test the direction and magnitude of N mineralization in the soil with plant invasion level, with the help of certain environmental changes. In this study, we conducted a time displacement experiment from uninvaded to invaded level, to study the effects of invasion-induced changes on soil N turnover. Higher quality and faster nutrient cycling rates of invasive species than natives have been recorded in previous studies [27]. Thus, we hypothesized that (1) the soil net N mineralization rates will increase with invasion. As the warming may accelerate the rates of N mineralization in the soil [28, 29], so we hypothesize that (2) the interacting effect of warming and plant invasion will greatly enhance mineralization rates of soil net N. Considering that the *S. canadensis* invasion did not cause the significant change of the richness and diversity of N-fixing microorganisms [30], we also hypothesize that (3) soil net N mineralization rates in the soil might be more sensitive to climate warming than plant invasion.

Material and Methods

Experiment Design

The experiment was carried out using the invasive *S. canadensis* (S) and native *Artemisia argyi* (A) – both belonging to the Asteraceae family, rhizomatous perennial plants, posing composite high stalk plants and the similar inhabit niches in China [31, 32]. The seeds of *S. canadensis* and *A. argyi* were collected from one population in a typical plant community dominated by these two plants in the suburb of Zhenjiang, China (119°51'E, 32°20'N) during the autumn season of 2016. On May 15, 2017, the seeds of *S. canadensis* and *A. argyi* were separately placed on the surface of the natural soil in garden pots kept in cultivation (diameter 24 cm; height 18 cm). Natural soil collected from the field sites where the two plants both growing

served as the substratum (TN: $747.10 \pm 14.90 \text{ mg Kg}^{-1}$, NO_3^- -N: $4.62 \pm 0.56 \text{ mg kg}^{-1}$, NO_4^+ -N: $36.20 \pm 13.77 \text{ mg kg}^{-1}$, pH: 4.5~6.0). When the plants had grown about 1cm in height (June 6, 2017), they were thinned to two invasion levels to represent ambient (uninvade, A3: three *A. argyi*) and invasion (invaded, S2A2: two *S. canadensis*+two *A. argyi*), respectively. Considering that productivity was constant in the pot while these two species saw unbalanced distribution in the field, we used different amounts of individuals in this experiment in order to highlight the uninvaded and invaded levels [33, 34].

The warming treatment was heated with a greenhouse [35], with windows and ventilators (380v, 2000w) installed at both ends for cross-ventilation [36, 37]. The control group was placed out of the greenhouse (ambient). To avoid the conditions different within and out of the greenhouse, the greenhouse was made of solar sheets with light transmittance of up to 96% [38, 39]. The air temperatures were recorded under ambient and warming conditions with data loggers (TH11R, HHW, China) at 10-min intervals during the course of the experiment [40].

There were a total of four manipulations in our experiment: ambient (CK, A3), invasion (S2A2, I), warming (A3+warming, W), and interact with invasion and warming (S2A2+warming, I+W). Each experimental manipulation was replicated 8 times. There were a total of 32 pots in our experiment and layout was randomized. During the period of the experimental setup, adequate tap water was supplied daily.

Soil Sampled

During the growing season (95 days after thinning, September 6, 2017), five rhizosphere soil samples of 0-15 cm depth were obtained following an S-shape in each pot after the litter and root were removed, and then it was well blended as suggested by Liu et al. [41]. One part of the sample was kept under the cold condition for transport back to the fridge and stored at 4°C for further analysis. Another part was air-dried, ground in

a planetary ball mill (Retsch MM400, Haan, German) and sieved to collect fractions with a particle diameter between 0.02 and 2 mm [42].

Physico-Chemical Measurements

The soil reaction (pH) was determined using a pH meter with a glass electrode in a soil-pure water suspension at a ratio of 1:2.5 [43]. The inorganic N (NH_4^+ -N and NO_3^- -N) was extracted the day after sampling with 1 M KCl in a fresh soil-to-solution ratio of 1:12.5 and shaking for 1-hr and extract analyzed calorimetrically using a UV-2600 flow injection analyzer (Shimadzu Corp., Japan) [10].

The activity of soil enzymes is a good indicator of soil biological properties [43], even representing the scope of nutrient cycling and the process of decomposition [44]. The activity of soil enzymes in our experiment was measured by using dry soil. Especially the activity of urease was measured based on urea visualized by phenol sodium hypochlorite, and also by the spectrophotometric determination of ammonium at 578 nm [45]. Urease activity was expressed as NH_4^+ -N released per gram of soil per hour [46]. The sucrase activity was determined by the 3,5-dinitrosalicylic acid anthracenone method and expressed as mg glucose g^{-1} soil 24 hr^{-1} [47]. The activity of catalase was determined by permanganate (KMnO_4) titration [44].

Calculation and Statistics

In our study, soil net N mineralization (SNmin) includes net mineralization (Nmin, inorganic N), net nitrification (NNmin, NO_3^- -N), and net ammonification (ANmin, NH_4^+ -N). The Nmin, NNmin, and ANmin as the difference between planting and harvest (end-start) in soil [48, 49]. All values were standard transformed using the min-max normalization method to satisfy the requirements of normality and homogeneity of variance. Data on the SNmin and enzyme were tested for the effects of warming or invasion with generalized linear models. Pearson's correlation and redundant analysis

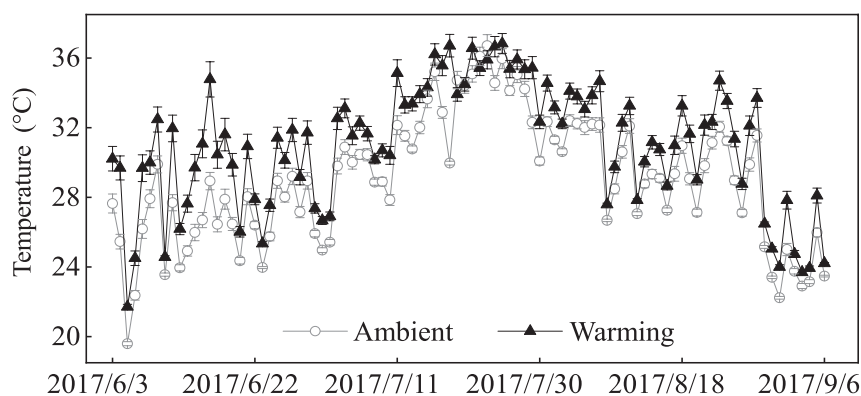


Fig. 1. Comparison of the daily average temperature for ambient and warming treatments during the 2017 growing season (daily data: mean \pm SE).

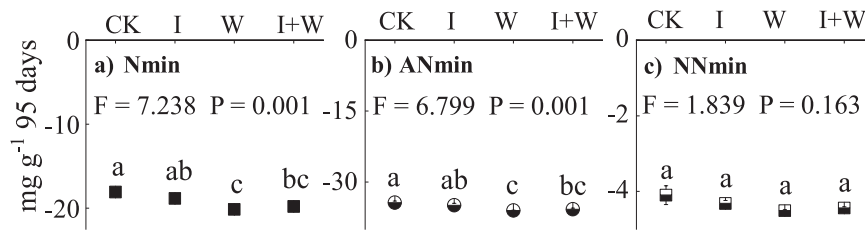


Fig. 2. Soil net N mineralization with manipulations. Where a) is net mineralization rate (Nmin), b) is net ammonium rate (ANmin), c) is net nitrification rate (NNmin); ambient, warming, and invasion were abbreviated as CK, W, and I; different letters indicate significance level at $P < 0.05$, and values represent the mean \pm SE.

(RDA) were also used for linking N mineralization and other factors (enzyme activities, pH, invasion, warming). Differences were considered significant when the t-test P-value was below type I error at $\alpha = 0.05$. All statistical analyses were performed using IBM SPSS Statistics 22.0 software (SPSS v2018, Chicago, IL, USA). All figures were drawn using Origin Pro 8.6 software (Originlab Co., Northampton, MA, USA).

Results and Discussion

Throughout the study period, mean temperature during warming treatment was $31.00 \pm 0.36^\circ\text{C}$, which was 1.98°C significantly higher than 29.02 ± 0.37 in the ambient ($P < 0.001$, Fig. 1). This increase successfully correlates with projected global warming by 2050 [50].

Net N Mineralization

The invasion and warming treatments in our experiment have a significant effect on the Nmin and

ANmin (all $P < 0.01$, Fig. 2a, b), while NNmin didn't show a significant change ($P = 0.163$, Fig. 2c). The Nmin shows a 4.21% decrease in an invasion than in the ambient, while they did not reach the significant level ($P = 0.132$, Fig. 2a). Treatment with the warming and interaction of invasion and warming had distinctly decreased by 11.40% and 9.46% in Nmin compare to ambient treatment, respectively ($P < 0.01$, Fig. 2a). The trend of ANmin and NNmin response to the invasion and warming was similar to Nmin (Fig. 2), the difference is that ANmin reached a significant level (Fig. 2b), while NNmin did not reach a significant level in warming and the interaction treatment compare to ambient treatment (Fig. 2c).

Enzyme and pH

Sucrase level was similar across all treatments ($P = 0.646$, Fig. 3a), and the content was increased to some extent and the highest was observed in warming treatment (12.954 ± 3.159 , Fig. 3a). The urease was not affected by the invasion ($P = 0.712$, Fig. 3b), while the warming and interaction of warming and invasion

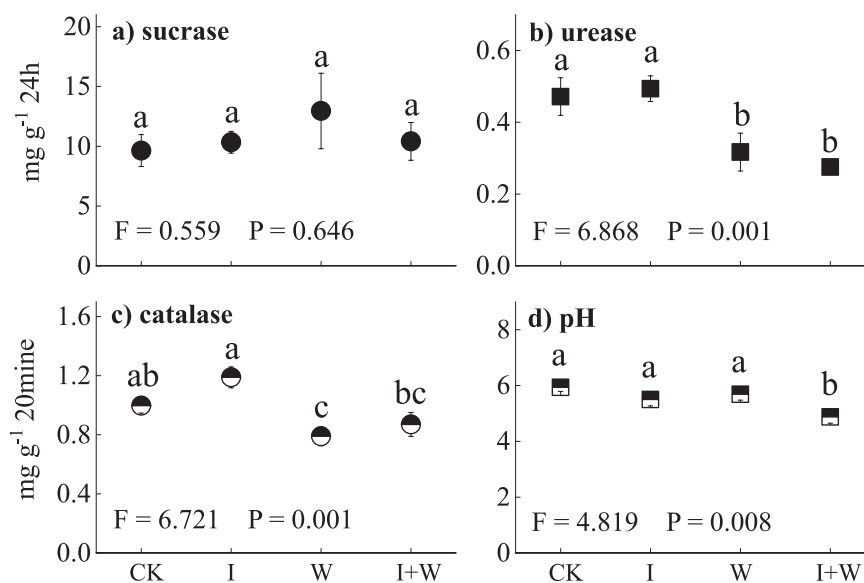


Fig. 3. Enzyme and pH with manipulations, where A is sucrase, B is urease, C is catalase, and D is pH; ambient, warming, and invasion were abbreviated as CK, W, and I; different letters indicate a significant level at $P < 0.05$, and values represent the mean \pm SE.

were significantly lower than ambient and invasion treatments (all $P < 0.01$, Fig. 3b). The difference from the warming treatment was a significant decrease in the catalase content compared to ambient and invasion treatments ($P < 0.05$, Fig. 3c), with the invasion treatment slightly increasing the content of catalase, while the interaction of invasion and warming showed a decrease to some extent (all $P > 0.05$, Fig. 3c). Neither invasion nor warming caused significant changes in pH, while they declined sharply in pH following their interaction (4.875 ± 0.227 , $P < 0.05$, Fig. 3d). Overall, urease, catalase, and pH were all sensitive to our experimental manipulations (all $P < 0.001$, Fig. 3), except sucrase.

Correlation Analysis

Correlation analysis was applied to the data in order to determine the relationship between the three kinds of N mineralization, enzymes, two environmental factors, and pH in this study. The results indicate that there was a significant positive correlation between the three kinds of net N mineralization ($P < 0.06$, Table 1). Sucrase was irrelevant with catalase ($P > 0.06$, Table 1), while both of them had a positive relationship with urease ($P < 0.06$, Table 1). Similarly, Nmin was a close relation to sucrase and urease ($P < 0.06$, Table 1). Catalase and pH did not show any relationship with other properties, except for urease and warming. The result was also shown that soil properties were repressed by warming ($P < 0.06$, Table 1), except for sucrase. However, the invasion was only negatively correlated with pH ($P < 0.01$, Table 1).

In the RDA of net mineralization rates of soil N with an environmental factor (enzyme activities, pH, invasion, warming) as the explanatory variables, Axis 1 (the x-axis) accounted for 37.9% of the variation in the dataset, with 1.9% of the variation accounted for by Axis 2 (the y-axis). Together, soil enzyme activities, pH, invasion, and warming explained 99.5% of the variation in the soil N mineralization (Fig. 4). Generally, warming has contributed more to the separation of the samples, as samples with ambient at the left-hand end

of the ordination, and samples with warming at the right-hand end of the ordination. The SNmin (Nmin, ANmin, NNmin) changed mainly along the direction of the x-axis, indicating that the environmental factors related to the x-axis were the main factors affecting soil mineralization. The patterns along the x-axis correlated positively with soil pH, enzymes and warming. Soil mineralization showed inconsistent responses to environmental factors. Whereas high Nmin, ANmin, and NNmin with high soil pH, catalase, and urease were found at the left-hand end of the ordination plots, while invasion, sucrase, and warming induces SNmin decreased (Fig. 4).

Net N Mineralization Did Not Increase with the Invasion

The soil of invaded stands had slightly lower SNmin than the control group, including Nmin, ANmin, and NNmin ($P > 0.05$, Fig. 2). All these data suggest lower rates of N cycling in the invaded stands. This result rejected our first hypothesis that the soil net N mineralization rates will increase with invasion, which may be because the litter biomass produced by plants growing in pots was generally low [51], thus restricting the role of litter decomposition in the N mineralization process. The exudation of chemical compounds via roots and nutrient uptake were different among various plant species [52], which will also contribute to the N mineralization and biological processes associated with N, but the rhizomes of invasive species did not form completely before harvesting [53], which thus limited the allelopathic effects into full play, even affecting the microbial activity and composition of the soil biota [54].

Net N Mineralization Decreased with Warming

Soil net N mineralization involves biological processes that are temperature-dependent [55].

Table 1. Pearson's correlation analysis among soil net N mineralization, enzyme activity, pH and environmental factors.

	Nmin	ANmin	NNmin	Sucrase	Catalase	Urease	pH	Warming
ANmin	0.920**							
NNmin	0.659**	0.366*						
Sucrase	-0.345*	-0.348*	-0.260					
Catalase	0.119	0.042	0.043	0.169				
Urease	0.344*	.222	0.305	0.358*	0.565**			
pH	0.262	0.227	0.111	-0.028	-0.073	0.119		
Warming	-0.613**	-0.497**	-0.345*	0.160	-0.597**	-0.641**	-0.325	
Invasion	-0.065	0.000	-0.098	-0.087	0.331	-0.034	-0.464**	0.000

**indicates the significant level at $P < 0.01$, * indicates the significant level at $P < 0.06$; Abbreviation: Nmin: net mineralization rate; ANmin: net ammonium rate; NNmin: net nitrification rate. Values are correlation coefficient.

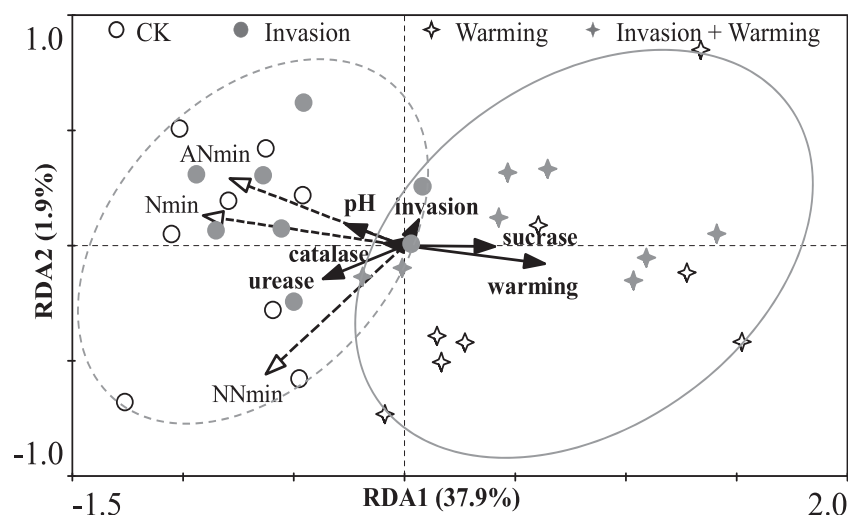


Fig. 4. Result of redundancy analysis (RDA) based on soil mineralization and impact factors (enzyme activities, pH, invasion, warming); Nmin is net mineralization rate, ANmin is net ammonium rate, and NNmin is net nitrification rate; samples in the same colors indicate sampling in the same treatment (black hollow circle: CK; gray solid circle: invasion; black hollow star: warming; gray solid star: invasion + warming).

Observations in our study showed a significant negative effect of warming on the SNmin, which was in contrast to the general belief that soil N mineralization rate increases with warming [1, 55, 56]. This could be primarily attributed to the high-temperature (more than 30°C) constraint on microbial activity, for example Zaman and Chang. [57] observed that nitrifying bacteria in agroforestry systems is optimal at or around 25°C. However, the lower NNmin at warming than at the ambient was in agreement with the results of the earlier findings showing that both net and gross nitrification rates declined with increasing temperature from 15 to 20°C [58]. These negative responses in NNmin to warming may be caused by the limited availability of soluble organic C in their soils [57], and the catalytic power of enzyme decreases with warming may also be a necessary reason [59]. The ANmin decreases with increasing soil temperature were also observed in [49], and were attributed to the lack of positive response in ammonification to increasing temperature to the accelerated immobilization of $\text{NH}_4^+\text{-N}$ by microbes [49, 60].

Net N Mineralization Response to the Interaction of Plant Invasion and Warming

Changes in environmental variability could significantly interact with other global change processes [9], such as biological invasions, an important element of global change [6]. Therefore, understanding of whether soil N turnover responds to warming varies with the invasion in the terrestrial ecosystem is essential for assessing soil N cycling and plant invasion [4]. Our results showed that temperature and invasion could interactively effect the SNmin process, strongly supporting our second hypothesis that the interacting

effect of warming and plant invasion will greatly enhance mineralization rates of soil net N, which may be because these two changes often as the controlling factor over soil microbes [40, 61], mycorrhizal colonization, and soil-plant feedback [62]. As the r-value in Pearson's analysis and the length of the arrow in RDA analysis indicates, the proportion of variability is explained by the variable [63, 64]. Therefore, from the correlation analysis, we observed that the N mineralization was more sensitive in warming than invasion level, which supported our third hypothesis that soil net N mineralization rates in the soil might be more sensitive to climate warming than plant invasion, and consistent with the magnitude of changes in soil microbial activities, gross N mineralization, nitrification rates, and net mineralization rates being much greater in response to temperature changes compared to the changes in soil moisture content or substrate type [57]. This may be due to:

1. The temperature in warming treatment significantly increasing by 1.98°C during the experimental period (Fig. 1), inducing the temperature beyond the optimum activity range for some key enzymes and microbes [57]. Therefore, the strong response in N turnover (SNmin decrease) to the experimental warming associated with the enzyme and microbes, which is sensitive to temperature [29].
2. Although invasive *S. canadensis* had positive allelopathic effects on its own growth [65], in our short-term cultured experiment, invasive species might not have had long enough residence time to exhibit its allelopathic effects into full play, especially for the rhizomes that did not form completely [53, 66, 67].
3. The soil organic matter content is lower, as the litter biomass produced by invasive plants growing in pots

was generally low [51]. Therefore, the soil N turnover was more sensitive in warming than invasion, and warming plays a key role when these two factors interact.

The Mechanism of Soil Net N Mineralization

Soil net N mineralization rate regulates the processes of N consumption (immobilization) and the production (mineralization) of N by microbial activity during incubation [58]. The negative values of Nmin, ANmin, and NNmin indicates that the N immobilization is larger than mineralization in our results (Fig. 2) [68]. Therefore, SNmin has no significant changes in invasion treatment, which may be because the *S. canadensis* invasion only alters the community structure, rather than the diversity and richness of soil N-fixing bacterial communities [30], and even some important soil physicochemical properties such as pH and enzyme also did not change (Fig. 3). While the richness of N functional microbial communities of the prairie was significantly affected by warming, especially for the *nirK*-harboring bacterial community, the richness was decreased and a structural change was observed after 1 year of warming [69]. These results are consistent with some previous analyses in soils, and the temperature plays a more primary role in shaping and controlling microbial growth, activities, and diversity than other proposed environment drivers, pH, N, and C [70, 71], also supported our third hypothesis to some extent.

Although we did not have the microbial data here, we measured the activity of soil enzymes from communities of bacteria and fungi. Enzymes act as a reliable, easy, and sensitive indicator of the quality and health status of the environment. It also relates to the trend and strength of the biochemical process, which directly or indirectly affects soil productivity, economy and ecosystem performance of organic matter degradation, mineralization of N or nitrification [72, 73]. Our results showed that the sucrase, catalase, and urease were decreased with invasion and warming, which may be correlated with the lower concentration of soil organic matter [74]. In addition, the enzyme activities are sensitive to temperature, and the different enzymes have a different optimum reaction temperature [43]. Pearson's correlation and RDA analysis showed that the net N mineralization strongly depended on urease and sucrase, which may be because of the urease and sucrase involved in N-cycle and C-cycle [72]. The catalase has no significant (limited) effect on N dynamic, which is consistent with the results under Agroforestry Systems in Northern Jiangsu Province [73]. The pH was negatively correlated with invasion (Table 1), which was also observed in the soil of *Amaranthus retroflexus* invasion sites [75]. The increase in pH will also directly stimulate nitrification by increasing the ratio of ammonia ($\text{NH}_3\text{-N}$) to ($\text{NH}_4^+\text{-N}$) [76, 77], even determining the relative proportion of

inorganic N that was nitrified [78]. Therefore, the decreased pH in manipulation must affect the SNmin in direct paths in our results (Table 1, Fig. 4), especially in the interaction of invasion and warming (Fig. 2).

Overall, Nmin, ANmin, and NNmin were not only suppressed by environmental factors, but also were affected by the enzyme and pH, which may even relate to N-fixing bacteria [30]. The previous study showed that ANmin and NNmin were significantly influenced by soil moisture and root biomass [49], and a significant positive correlation was also found between Nmin and fine-root biomass [48]. It was reported that the increase in fine-root biomass can lead to the increase of root-derived C, which is coupled with stimulating microbial activity and accelerating N transformation in the soils [79], even affecting the C:N soil [80]. Therefore, the decrease of SNmin with *S. canadensis* invasion and climate warming may result in the N mineralization and transformation processes slowing down, thereby exacerbating the shortage of nitrogen and species competition. In general, the invasive species possess the stronger environmental adaptability and capacity for nutrients compared with native species [20, 81], which would lead invasive species invasions to be more successful under the condition of an N shortage induced by plant invasion and climate warming.

Conclusions

The study presented here examined the invasion, warming and their interactive effect on soil net N mineralization. The results suggest that a complete conversion from uninvaded pots to *S. canadensis* invasion would slightly reduce the net N mineralization rates. However, the presence of warming significantly decrease the net N mineralization rates at both uninvaded and invaded pots. These results are tightly related to the pH and enzyme in soil, and may also be related to the litter production and allelopathic effects in the plant. Therefore, the environmental changes in plant invasion and climate warming, and the subsequent decreased net N mineralization in soil that would be a possible decrease the nutrient source for vegetation [82], even exacerbate species competition and feedback on other ecological processes. However, those aspects may have been considerably incomplete so far. All need to be studied further.

Acknowledgements

This work was supported by the State Key Research Development Program of China (2017YFC1200100), National Natural Science Foundation of China (31770446, 31570414, 31600326, 31800342), the Priority Academic Pro-gram Development of Jiangsu Higher Education Institutions (PAPD) China Postdoctoral Science Foundation (2019M651720), China Postdoctoral

Science Foundation (2019M651720), the Jiangsu province Postdoctoral Science Foundation (1501014B), the Jiangsu Collaborative Innovation Center of Technology and Material of Water Treatment, and Study Abroad Scholarship of Jiangsu University.

Author Contributions

Daolin Du and Zhicong Dai designed the experiment. Guangqian Ren and Min He performed the experiment. Qiong Ran and Zhicong Dai collected the data. Guanlin Li and Zhiyuan Hu analyzed the data. Guangqian Ren, A. Anandkumar and Chris B Zou wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest

The author declares no conflict of interest.

References

- RUSTAD L., CAMPBELL J., MARION G., NORBY R., MITCHELL M., HARTLEY A., CORNELISSEN J., GUREVITCH J., GCTE N. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*. **126** (4), 543, **2001**.
- LU X.M., EVAN SIEMANN XU S., HUI W., JIAN QING D. Climate warming affects biological invasions by shifting interactions of plants and herbivores. *Global Change Biol.* **19** (8), 2339, **2013**.
- MA Z., LIU H., MI Z., ZHANG Z., WANG Y., XU W., JIANG L., HE J. Climate warming reduces the temporal stability of plant community biomass production. *Nat. Commun.* **8**, 15378, **2017**.
- LI Z., ZHANG L., BANGLIANG D., YUANQIU, L., FANQIAN K., GUOXIAN H., QIN Z., QIAN L., XIAOMIN G., YANQIU F., DEKUI N., EVAN S. Effects of moso bamboo (*Phyllostachys edulis*) invasions on soil nitrogen cycles depend on invasion stage and warming. *Environ. Sci. Pollut. Res.* **24** (32), 24989, **2017**.
- PALMER J.G., TURNEY C.S.M., FOGWILL C., FENWICK P., THOMAS Z., JONES R.T., BEAVEN B., RICHARDSON S.J., LIPSON M. Growth response of an invasive alien species to climate variations on subantarctic Campbell Island. *N. Z. J. Ecol.* **42** (1), 31, **2017**.
- DUKES J.S., MOONEY H.A. Does global change increase the success of biological invaders? *Trends Ecol. Evol.* **14** (4), 135, **1999**.
- HULME P.E., LE ROUX J.J. Invasive species shape evolution. *Science*. **352** (6284), 422, **2016**.
- YUAN J., DING W., LIU D., KANG H., FREEMAN C., XIANG J., LIN Y. Exotic *Spartina alterniflora* invasion alters ecosystem-atmosphere exchange of CH₄ and N₂O and carbon sequestration in a coastal salt marsh in China. *Global Change Biol.* **21** (4), 1567, **2015**.
- PAREPA M., FISCHER M., BOSSDORF O. Environmental variability promotes plant invasion. *Nat. Commun.* **4**, 1604, **2013**.
- XIONG Q., PAN K., ZHANG L., WANG Y., LI W., HE X., LUO H. Warming and nitrogen deposition are interactive in shaping surface soil microbial communities near the alpine timberline zone on the eastern Qinghai-Tibet Plateau, southwestern China. *Appl. Soil Ecol.* **101**, 72, **2016**.
- PAN P., ZHAO F., NING J., ZHANG L., OUYANG X., ZANG, H. Impact of understory vegetation on soil carbon and nitrogen dynamic in aerially seeded *Pinus massoniana* plantations. *PLoS One*. **13** (1), e0191952, **2018**.
- SEEBENS H., ESSL F., DAWSON W., FUENTES N., MOSER D., PERGL J., PYSEK P., VAN KLEUNEN M., WEBER E., WINTER M., BLASIUS B. Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biol.* **21** (11), 4128, **2015**.
- GALLARDO B., CLAVERO M., SANCHEZ M.I., VILA M. Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biol.* **22** (1), 151, **2016**.
- JACKSON R.B., BANNER J.L., JOBB GY E.G., POCKMAN W.T., WALL D.H. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*. **418** (6898), 623, **2002**.
- AANDERUD Z.T., BLEDSOE C.S. Preferences for 15N-ammonium, 15N-nitrate, and 15N-glycine differ among dominant exotic and subordinate native grasses from a California oak woodland. *Environ. Exp. Bot.* **65** (2-3), 205, **2009**.
- CORBIN J.D., D'ANTONIO C.M. Effects of exotic species on soil nitrogen cycling: Implications for restoration. *Weed Technol.* **18** (sp1), 1464, **2004**.
- BALDOCK J.A., SKJEMSTAD J.O., DERENNE S., KNICKER H. Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Org. Geochem.* **31** (7), 697, **2000**.
- REICH P.B., GRIGAL D.F., ABER J.D., GOWER, S.T. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology*. **78** (2), 335, **1997**.
- HAFDAHL C.E., CRAIG T.P. Flowering phenology in *Solidago altissima*: adaptive strategies against temporal variation in temperature. *J. Plant Interact.* **9** (1), 122, **2013**.
- WAN L.Y., QI S.S., ZOU C.B., DAI Z.C., ZHU B., SONG Y.G., DU D.L. Phosphorus addition reduces the competitive ability of the invasive weed *Solidago canadensis* under high nitrogen conditions. *Flora*. **240**, 68, **2018**.
- WERNER P.A., BRADBURY I.K., GROSS R.S. The biology of canadian weeds. 45. *solidago canadensis* L. *Can. J. Plant. Sci.* **60** (4), 1393, **1980**.
- WEBER E. Morphological variation of the introduced perennial *Solidago canadensis* L. *sensu lato* (Asteraceae) in Europe. *Bot. J. Linn. Soc.* **123** (3), 197, **1997**.
- SUN B.Y., TAN J.Z., WAN Z.G., GU F.G., ZHU M.D. Allelopathic effects of extracts from *Solidago canadensis* L. against seed germination and seedling growth of some plants. *J. Environ. Sci.* **18** (2), 304, **2006**.
- WANG C., WU B., JIANG K., ZHOU J., DU D. Canada goldenrod invasion affect taxonomic and functional diversity of plant communities in heterogeneous landscapes in urban ecosystems in East China. *Urban For Urban Gree.* **38**, 145, **2019**.
- LIAO C., PENG R., LUO Y., ZHOU X., WU X., FANG C., CHEN J., LI B. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol.* **177** (3), 706, **2008**.

26. VALLIERE J.M., IRVINE I.C., SANTIAGO L., ALLEN E.B. High N, dry: Experimental nitrogen deposition exacerbates native shrub loss and nonnative plant invasion during extreme drought. *Global Change Biol.* **23** (10), 4333, **2017**.
27. SARDANS J., BARTRONS M., MARGALEF O., GARGALLO-GARRIGA A., JANSSENS I.A., CIAIS P., OBERSTEINER M., SIGURDSSON B.D., CHEN H.Y., PENUELAS J. Plant invasion is associated with higher plant-soil nutrient concentrations in nutrient-poor environments. *Global Change Biol.* **23** (3), 1282, **2017**.
28. DOIRON M., GAUTHIER G., L VESQUE E., NEWMAN J. Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. *J. Ecol.* **102** (2), 508, **2014**.
29. BLAGODATSKAYA E., KHOMYAKOV N., MYACHINA O., KUZYAKOV Y. Temperature sensitivity and enzymatic mechanisms of soil organic matter decomposition along an altitudinal gradient on Mount Kilimanjaro. *Sci Rep.* **6**, 22240, **2016**.
30. WANG C., JIANG K., ZHOU J., WU B. *Solidago canadensis* invasion affects soil N-fixing bacterial communities in heterogeneous landscapes in urban ecosystems in East China. *Sci. Total Environ.* **631-632**, 702, **2018**.
31. LI J., DU L., GUAN W., YU F.H., VAN KLEUNEN M. Latitudinal and longitudinal clines of phenotypic plasticity in the invasive herb *Solidago canadensis* in China. *Oecologia.* **182** (3), 755, **2016**.
32. S RBU C., OPREA A. New records in the alien flora of Romania (*Artemisia argyi*, *A. lavandulaefolia*) and Europe (*A. lancea*). *Turk. J. Bot.* **35** (6), 717, **2011**.
33. BRACKEN M.E.S., STACHOWICZ J.J. Seaweed diversity enhances nitrogen uptake via complementary use of nitrate and ammonium. *Ecology.* **87** (9), 2397, **2006**.
34. GRIFFIN J.N., HAYE K.L.D.L., HAWKINS S.J., JENKINS T.S.R. Predator diversity and ecosystem functioning: density modifies the effect of resource partitioning. *Ecology.* **89** (2), 298, **2008**.
35. GIBSON D.J., CONNOLLY J., HARTNETT D.C., WEIDENHAMER J.D. Designs for greenhouse studies of interactions between plants. *J. Ecol.* **87** (1), 1, **1999**.
36. TEITEL M., ATIAS M., BARAK M. Gradients of temperature, humidity and CO₂ along a fan-ventilated greenhouse. *Biosyst. Eng.* **106** (2), 166, **2010**.
37. VALI O.V., RASHEED A., TARQUIS A.M., PERDIGONES, A. Effect of increasing temperatures on cooling systems. A case of study: European greenhouse sector. *Clim. Change.* **123** (2), 175, **2014**.
38. DING X., ZHOU C. Test and measurement of solar visible radiation transmittance of greenhouse glazing. *Transactions of the CSAE.* **24** (8), 210, **2008**.
39. RA L., U.S., NGEL J.C.F., JOS P.A., ÁNGEL C.O. Greenhouse tomato production with electricity generation by roof-mounted flexible solar panels. *Scientia Agricola.* **69** (4), 233, **2012**.
40. FANG X., ZHOU G., LI Y., LIU S., CHU G., XU Z., LIU J. Warming effects on biomass and composition of microbial communities and enzyme activities within soil aggregates in subtropical forest. *Biol. Fertil. Soils.* **52** (3), 353, **2015**.
41. LIU X.S., SIEMANN E., CUI C., LIU Y.Q., GUO X.M., ZHANG L. Moso bamboo (*phyllostachys edulis*) invasion effects on litter, soil and microbial pfla characteristics depend on sites and invaded forests. *Plant Soil.* **2019**.
42. ROSLING A., LINDAHL B.D., FINLAY R.D. Carbon allocation to ectomycorrhizal roots and mycelium colonising different mineral substrates. *New Phytol.* **162** (3), 795, **2004**.
43. KUSCU I.S.K. Changing of soil properties and urease-catalase enzyme activity depending on plant type and shading. *Environ Monit Assess.* **191** (3), 178, **2019**.
44. HUANG D., XUE W., ZENG G., WAN J., CHEN, G., HUANG C., ZHANG C., CHENG M., XU P. Immobilization of Cd in river sediments by sodium alginate modified nanoscale zero-valent iron: Impact on enzyme activities and microbial community diversity. *Water Res.* **106**, 15, **2016**.
45. HU B., LIANG D., LIU J., LEI L., YU D. Transformation of heavy metal fractions on soil urease and nitrate reductase activities in copper and selenium co-contaminated soil. *Ecotoxicol Environ Saf.* **110**, 41, **2014**.
46. ARAG N R., SARDANS J., PE UELAS J. Soil enzymes associated with carbon and nitrogen cycling in invaded and native secondary forests of northwestern Argentina. *Plant Soil.* **384** (1-2), 169, **2014**.
47. WU H., XU J., WANG J., QIN X., WU L., LI Z., LIN S., LIN W., ZHU Q., KHAN M.U., LIN W. Insights into the mechanism of proliferation on the special microbes mediated by phenolic acids in the *Radix pseudostellariae* rhizosphere under continuous monoculture regimes. *Front. Plant Sci.* **8**, 659, **2017**.
48. XIAO Y.L., TU L.H., CHEN G., PENG Y., HU H.L., HU T.X., LIU L. Soil-nitrogen net mineralization increased after nearly six years of continuous nitrogen additions in a subtropical bamboo ecosystem. *J. For. Res.* **26** (4), 949, **2015**.
49. FU W., WANG X., WEI X.R. No response of soil N mineralization to experimental warming in a northern middle-high latitude agro-ecosystem. *Sci. Total Environ.* **659**, 240, **2019**.
50. ROGELJ J., MEINSHAUSEN M., KNUTTI R. Global warming under old and new scenarios using IPCC climate sensitivity range estimates. *Nat. Clim. Change.* **2** (4), 248, **2012**.
51. STEFANOWICZ A.M., MAJEWSKA M.L., STANEK M., NOBIS M., ZUBEK S. Differential influence of four invasive plant species on soil physicochemical properties in a pot experiment. *J. Soils Sediments.* **18** (4), 1409, **2017**.
52. SEMCHENKO M., SAAR S., LEPIK A. Intraspecific genetic diversity modulates plant-soil feedback and nutrient cycling. *New Phytol.* **216** (1), 90, **2017**.
53. REN G.Q., LI Q., LI Y., LI J., MICHAEL O.A., DAI Z.C., LI G.L., WAN L.Y., ZHANG B., ZOU C.B., RAN Q., DU D.L. The enhancement of root biomass increases the competitiveness of an invasive plant against a co-occurring native plant under elevated nitrogen deposition. *Flora.* **261**, 151486, **2019**.
54. CASTRO-DIEZ P., GODOY O., ALONSO A., GALLARDO A., SALDANA A. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecol Lett.* **17** (1), 1, **2014**.
55. DALIAS P., ANDERSON J.M., BOTTLNER P., COÛTEAUX, M. Temperature responses of net nitrogen mineralization and nitrification in conifer forest soils incubated under standard laboratory conditions. *Soil Biol. Biochem.* **34** (5), 691, **2002**.
56. WANG C., WAN S., XING X., ZHANG L., HAN X. Temperature and soil moisture interactively affected soil net N mineralization in temperate grassland in Northern China. *Soil Biol. Biochem.* **38** (5), 1101, **2006**.
57. ZAMAN M., CHANG S.X. Substrate type, temperature, and moisture content affect gross and net N mineralization

- and nitrification rates in agroforestry systems. *Biol. Fertil. Soils*. **39** (4), 269, **2004**.
58. STOTTLEMYER R., TOCZYDLOWSKI D. Nitrogen mineralization in a mature boreal forest, Isle Royale, Michigan. *J. Environ. Qual.* **28** (2), 709, **1999**.
 59. ALVAREZ G., SHAHZAD T., ANDANSON L., BAHN M., WALLENSTEIN M.D., FONTAINE S. Catalytic power of enzymes decreases with temperature: New insights for understanding soil C cycling and microbial ecology under warming. *Global Chang Biol.* **2018**.
 60. BENGTSSON G., BENGTSON P., MANSSON K.F. Gross nitrogen mineralization-, immobilization-, and nitrification rates as a function of soil C/N ratio and microbial activity. *Soil Biol. Biochem.* **35** (1), 143, **2003**.
 61. WANG C., XIAO H., LIU J., WANG L., DU D. Insights into ecological effects of invasive plants on soil nitrogen cycles. *AJPS*. **06** (01), 34, **2015**.
 62. WHEELER J.A., FREY S.D., STINSON K.A. Tree seedling responses to multiple environmental stresses: Interactive effects of soil warming, nitrogen fertilization, and plant invasion. *For. Ecol. Manage.* **403**, 44, **2017**.
 63. ANWAR E., YAN Z.B., TIAN D., HAN W.X., TANG Z.Y., FANG J. Drought effect on plant biomass allocation: A meta-analysis. *Ecol. Evol.* **7** (24), 11002, **2017**.
 64. KENNEDY N., CONNOLLY J., CLIPSON N. Impact of lime, nitrogen and plant species on fungal community structure in grassland microcosms. *Environ. Microbiol.* **7** (6), 780, **2005**.
 65. ADOMAKO M.O., NING L., TANG M., DU D.-L., VAN KLEUNEN M., YU F.-H. Diversity- and density-mediated allelopathic effects of resident plant communities on invasion by an exotic plant. *Plant Soil*. **2019**.
 66. POELMAN M.E., PILMANIS A.M., HUFFORD K.M. Testing the cultivar vigor hypothesis: comparisons of the competitive ability of wild and cultivated populations of *Paspalum smithii* along a restoration chronosequence: cultivar persistence in restoration. *Restor. Ecol.*, 10.1111/rec.12822, **2018**.
 67. BEZENG B.S., MORALES-CASTILLA I., MICHELLE V.D.B., YESSOUFOU K., DARU B. H., DAVIES T.J. Climate change may reduce the spread of non-native species. *Ecosphere*. **8** (3), e01694, **2017**.
 68. SCHMIDT I.K., JONASSON S., MICHELSEN A. Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. *Appl. Soil Ecol.* **11** (2-3), 147, **1999**.
 69. PENTON C.R., ST LOUIS D., PHAM A., COLE J.R., WU L., LUO Y., SCHUUR E.A., ZHOU J., TIEDJE J.M. Denitrifying and diazotrophic community responses to artificial warming in permafrost and tallgrass prairie soils. *Front. Microbiol.* **6**, 746, **2015**.
 70. ZHOU J., DENG Y., SHEN L., WEN C., YAN Q., NING D., QIN Y., XUE K., WU L., HE Z., VOORDECKERS J.W., NOSTRAND J.D., BUZZARD V., MICHALETZ S.T., ENQUIST B.J., WEISER M.D., KASPARI M., WAIDE R., YANG Y., BROWN J.H. Temperature mediates continental-scale diversity of microbes in forest soils. *Nat. Commun.* **7**, 12083, **2016**.
 71. DAVIDSON E.A., JANSSENS I.A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*. **440** (7081), 165, **2006**.
 72. RAO M.A., SCELZA R., ACEVEDO F., DIEZ M.C., GIANFREDA L. Enzymes as useful tools for environmental purposes. *Chemosphere*. **107**, 145, **2014**.
 73. WAN F., CHEN P. Soil enzyme activities under agroforestry systems in Northern Jiangsu Province. *Forest. Stu. in China*. **6** (2), 21, **2004**.
 74. WANG G., CAO F. Integrated evaluation of soil fertility in Ginkgo (*Ginkgo biloba* L.) agroforestry systems in Jiangsu, China. *Agrofor. Syst.* **83** (1), 89, **2011**.
 75. WANG C.Y., ZHOU J.W., LIU J., DU D.L. Responses of soil N-fixing bacteria communities to invasive species over a gradient of simulated nitrogen deposition. *Ecol. Eng.* **98**, 32, **2017**.
 76. BOER W.D., KOWALCHUK G.A. Nitrification in acid soils: micro-organisms and mechanisms. *Soil Biol. Biochem.* **33** (7-8), 0, **2001**.
 77. BOLLMANN A., LAANBROEK H.J. Continuous culture enrichments of ammonia-oxidizing bacteria at low ammonium concentrations. *FEMS Microbiol. Ecol.* **37** (3), 211, **2001**.
 78. HANAN E.J., SCHIMEL J.P., DOWDY K., D'ANTONIO C.M. Effects of substrate supply, pH, and char on net nitrogen mineralization and nitrification along a wildfire-structured age gradient in chaparral. *Soil Biol. Biochem.* **95**, 87, **2016**.
 79. YIN H., LI Y., XIAO J., XU Z., CHENG X., LIU Q. Enhanced root exudation stimulates soil nitrogen transformations in a subalpine coniferous forest under experimental warming. *Global Change Biol.* **19** (7), 2158, **2013**.
 80. LI G., HAN X., HUANG J. N mineralization and nitrification in a primary *Lithocarpus xylocarpus* forest and degraded vegetation in the Ailao Mountain, Yunnan Province. *Acta Botanica Sinica*. **46** (2), 194, **2004**.
 81. LIU Y.J., ODUOR A.M.O., ZHANG Z., MANEAS A., TOOTH I.M., LEISHMANS M.R., XU X.L., KLEUNE M.V. Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biol.* **23** (8), 3363, **2017**.
 82. SHIBATA H., HASEGAWA Y., WATANABE T., FUKUZAWA K. Impact of snowpack decrease on net nitrogen mineralization and nitrification in forest soil of northern Japan. *Biogeochemistry*. **116** (1-3), 69, **2013**.