Nitrogen addition frequency and propagule pressure influence *Solidago canadensis* invasion into native plant community

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**ABSTRACT**

**Introduction:** Propagule pressure (i.e., the number of propagules) has long been recognized to play an essential role in plant invasion. But it is not clear whether propagule pressure influences the invasion of exotic plants into native plant communities when different frequencies of nitrogen are added.

**Method:** We established an experiment with three plant communities that included native plant communities alone (four grasses, two legumes and two forbs) or native plant communities with one or five invasive plants, *Solidago canadensis*, under three frequencies of nitrogen addition (no addition or low or high addition with the same amount).

**Results:** High propagule pressure significantly enhanced the biomass and relative dominance index of *S. canadensis*. Moreover, high propagule pressure only decreased the total and aboveground biomass of the legumes. However, the competitive effect between *S. canadensis* and the native community and biomass of the whole native community varied according to different frequencies.

**Conclusion:** Overall, high propagule pressure encouraged invasion by *S. canadensis*, while low nitrogen frequency was advantageous for the native community to resist invasion in this experiment. The results provide a scientific basis to manage and control the invasion of *S. canadensis*.

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Another important factor for invasion success is the environment of invaded area, such as the availability of nitrogen (Yuan, Guo, and Ding et al. 2003; Britton and Fisher 2007; Elser, Bracken, and Cleland et al. 2007; Hwang and Lauenroth 2008). As is well known, nitrogen can restrict the growth and reproduction of plants (Bozzolo and Lipsn 2013). Nitrogen is usually released at different frequencies in nature, which results in heterogeneous distribution (Hodge 2004; Lamb, Stewart and Cahill 2012; Ling, XueMei, and XueJun 2012). Owing to the heterogeneity of atmospheric nitrogen deposition and sensitivity of different plants to nitrogen, there is still a high degree of uncertainty of the relationship between nitrogen deposition and plant invasion (Bradley, Blumenthal, and Wilcove et al. 2010). The addition of N, primarily ammonium salt and nitrate, is typically used to simulate nitrogen deposition in the atmosphere. Previous studies have shown that increasing the frequency of nitrogen addition can promote some growth and facilitate interspecific competition with native communities (Gebauer and Ehleringer 2000; Gebauer, Schwinning, and Ehleringer 2002; James and Richards 2007). However, other studies have not found this to be the case (Song, Bao, and Liu et al. 2012; Wang, Jiang, and Zhang et al. 2015). Furthermore, other research revealed the responses of invasive plants and native communities to pulses of nitrogen. In particular, nitrogen pulses increased the species richness and competitiveness of annual invasive herbs (Siemann and Rogers 2007; Mazzola, Chambers, and Blank et al. 2011) and promoted the spread of alien species (Li, Lei, and Zhi et al. 2011; Wang, Chen, and Yan et al. 2019; Q, Y, and Li et al. 2020). However, previous studies have rarely explored the impact of frequency of nitrogen addition on plant invasion and native plants under different propagule pressures.

**Solidago canadensis** L., which is strongly invasive and widely distributed, is one of the most destructive invasive clonal herbs in southeastern China. Its belowground part consists of a transverse rhizome, which produces extensive root systems that enlarge the population through vegetative propagation (Dong, Lu, and Zhang et al. 2005; Hartnett and Bazzaz 1985). They then compete with native species for resources and become the dominant species (Gusev 2015). There were some invasional mechanism about *S. canadensis*, the researches about the impact of frequency of nitrogen addition on plant invasion into native plant community under different propagule pressures were rare.

Thus, we chose the invasive plant *S. canadensis* as the focal species for a greenhouse experiment. We simulated the invasion of *S. canadensis* into a native plant community that consisted of eight native terrestrial plant species of three functional groups (grasses, legumes, and forbs) under three levels of propagule pressure and three frequencies of nitrogen addition. The goal was to test whether propagule pressure or the frequency of nitrogen addition would promote the invasion of the exotic plant *S. canadensis* into a native plant community. We sought to address the following questions: (1) Does the increased propagule pressure promote *S. canadensis* invasion? (2) Do different frequencies of nitrogen addition affect the resistance of native communities to invasion by *S. canadensis*? And (3) Does the impact of propagule pressure on *S. canadensis* invasion vary with different nitrogen frequencies?

**Materials and methods**

**Plant preparation**

Seeds of *S. canadensis* were collected from the suburbs of Hangzhou, Zhejiang Province, China, and were planted in the greenhouse at Forest Science Co., Ltd., of Beijing Forestry University (Beijing, China) (40°40′33″ N, 116°20′24″ E).

Eight local species, which are commonly found in northern China and have the same root system as *S. canadensis*, were selected as the constructed plant communities, including four grasses (*Lolium perenne, Bromus inermis, Poa pratensis*, and *Festuca arundinacea*), two legumes (*Trifolium repens* and *T. pretense*), and two non-grass broadleaf herbs (*Ixeris denticulate* and *Cichorium intybus*). The seeds of native species were purchased from China Vegetable Seed Technology Co. Ltd. (Beijing, China).

**Experimental design**

We established three propagule pressure treatments, including a native plant community alone and native plant communities with one or five *S. canadensis* individuals, crossed with three frequencies of nitrogen addition, including no addition, and low (every 15 days) or high (every 5 days) addition with the same amount of nitrogen. There were nine treatments with six replicates per treatment. Each replicate was distributed randomly among a plastic container (diameter, 27 cm; height, 34 cm) filled 22 cm high with a mixture of vermiculite, river sand, and peat (1:1:1 [v/v/v]).

On 4 May 2016, we constructed 54 artificial native plant communities by transplanting eight native plants. One week later, we selected several similarly sized seedlings of *S. canadensis* transplanted at the same time. We designated the transplantation of one or five seedlings of *S. canadensis* into the native plant community as low or high propagule pressure, respectively, and the native plant community alone as the no-invasion treatment. The native plant community included one individual each of the eight native plant species.

One week after *S. canadensis* was planted, nitrogen was added in the form of ammonium nitrate (NH$_4$NO$_3$). We dissolved the ammonium nitrate in deionized water and sprayed it on the plant and soil surface
(He, Yu, and Sun 2011; Li, Ning, and Alpert et al. 2014). A volume of 200 mL of deionized water was sprayed as the control. The low frequency nitrogen treatment involved the addition of 200 mL of 0.066 g water-soluble ammonium nitrate every 15 days for a total of six times. The high frequency treatment consisted of the addition of 200 mL of 0.022 g water-soluble ammonium nitrate every five days for a total of 18 times (Figure 1). The experiment was designed to simulate precipitation and atmospheric nitrogen deposition in sampled areas (Zhou, Li, and Luo et al. 2009). The total amount of nitrogen added for the frequency treatment was 10 g/m-2·a-1. The experiment was conducted in the greenhouse for 90 days from May 4 to 4 August 2016.

**Measurements**

We harvested all the individual *S. canadensis* plants and measured their stem lengths and numbers of leaves. All the *S. canadensis* materials were then brought back to the laboratory, and the leaf areas were determined by scanning the leaves and analyzing them with WinFOLIA (Pro2004a; Regent Instruments, Québec, Canada). The native species were harvested as three functional groups, including the legumes, grasses, and non-grass broadleaf herbs. All the plants were separated into two parts (aboveground and belowground) and weighed after oven drying at 70°C for more than 48 hours.

**Statistical analysis**

**Data calculation**

We calculated the competitive effect (CE) on native plant communities (Liu, Quan, and Dong et al. 2016) as follows:

\[
CE = \ln \left( \frac{R_D}{R_W} \right)
\]

Where, \(R_D\) is the biomass of native communities alone, and \(R_W\) is the biomass of native communities after invasion. A positive value suggests competition between *S. canadensis* and the native plant community, while a negative value indicates that *S. canadensis* invasion promotes the growth of native plant community.

We then calculated the relative dominance index (RDI) of *S. canadensis* (Liu, Quan, and Dong et al. 2016) (Lei, Wang, and Feng et al. 2012).

\[
RDI = \frac{A}{A + B}
\]

A is the biomass of *S. canadensis*, and B is the biomass of eight native plants.

**Analytical data programs**

A two-way analysis of variance (ANOVA) was performed to examine the effects of propagule pressure, nitrogen addition and their interaction on plant growth, and the relationship between invasive species and native communities. A Duncan test was used for multiple comparisons after the detection of significant effects. Tests of normality and homogeneity of variance were performed before analysis. The data were transformed to the natural log or square root before analysis when necessary to remove heteroscedasticity. SPSS 19.0 (IBM, Inc., Armonk, NY, USA) was used to conduct the analyses, and SigmaPlot 12.5 (Systat Software, Inc., San Jose, CA, USA) was used for graphics.

**Results**

**The growth of *S. canadensis***

Propagule pressure significantly affected all the growth indices of *S. canadensis* (Table 1A, \(P < 0.05\)), while the frequencies of nitrogen addition and interaction between the two treatments both did not affect the growth traits of *S. canadensis* (Table 1A). High propagule pressure significantly increased all the growth indices of *S. canadensis* (Figure 2). Although not significant, all the growth indices of *S. canadensis* improved following treatment with a high frequency of nitrogen (Figure 2). At the individual level, the frequency of nitrogen addition, propagule pressure and their interaction had no significant effect on several growth indices of *S. canadensis* (Table S1; Fig. S1).

**The growth of native plant communities**

The frequencies of nitrogen addition significantly affected all the belowground and total biomass of the native communities (Table 1B, \(P < 0.05\)), while propagule pressure and interaction between the two treatments did not affect the biomass of native communities (Table 1B). The belowground biomass and total biomass of native communities improved following treatment with a low frequency of nitrogen addition, and it decreased under a high nitrogen frequency.
Table 1. Summary of ANOVAs for the effects of nitrogen addition (N) and propagule pressure (P) on Solidago canadensis and native communities.

|                         | N   | P   | N × P |
|-------------------------|-----|-----|-------|
| **A. S. canadensis**    |     |     |       |
| Leaf area               | 0.37| 0.693|16.76  |
| Number of leaves        | 1.03| 0.370|45.84  |
| Stem length             | 0.13| 0.875|50.76  |
| Leaf biomass            | 0.71| 0.499|16.52  |
| Root biomass*           | 1.53| 0.233|17.39  |
| Stem biomass            | 0.77| 0.471|14.15  |
| Aboveground biomass     | 0.74| 0.486|16.06  |
| Total biomass           | 0.89| 0.423|16.52  |
| **B. Native communities**|   |     |       |
| Total biomass           | 3.44| 0.041|0.32   |
| Aboveground biomass     | 3.11| 0.054|0.34   |
| Belowground biomass     | 4.05| 0.024|0.14   |
| **C. Legumes**          |     |     |       |
| Total biomass           | 1.95| 0.154|4.22   |
| Aboveground biomass     | 1.30| 0.283|5.05   |
| Belowground biomass     | 2.34| 0.108|3.18   |
| **D. Grass**            |     |     |       |
| Total biomass*          | 1.23| 0.302|1.72   |
| Aboveground biomass     | 1.22| 0.306|1.53   |
| Belowground biomass     | 1.03| 0.366|2.97   |
| **E. Non-grass broadleaf herbs** |   |     |       |
| Total biomass           | 1.92| 0.158|1.15   |
| Aboveground biomass     | 1.73| 0.189|1.19   |
| Belowground biomass     | 2.55| 0.089|0.66   |

*indicates square root-transformed data. Significant values of F and P are shown in bold. ANOVA, analysis of variance.

(Figure 3A,C). Although not significant, the frequencies of nitrogen addition affected the aboveground biomass in a similar manner (Figure 3B).

At the function group level, propagule pressure only affected the aboveground and total biomass of the legumes (Table 1C, P < 0.05). However, the belowground biomass of legumes and all the biomass of grass and forbs were not affected by propagule pressure (Table 1C-E). The aboveground and total biomass of the legumes significantly decreased as the level of pressure of S. canadensis propagules increased (Figure 4A,D). Simultaneously, the frequency of nitrogen addition did not affect any biomass indices of all the functional groups (Table 1C-E).

**Interactions between S. canadensis and the native plant community**

Propagule pressure significantly increased the relative dominance index (RDI) of S. canadensis (Table 2, P < 0.05, Figure 5B), while it did not significantly affect the competitive effect (CE) (Table 2). Although the frequencies of nitrogen addition and interaction between the two treatments did not significantly affect the RDI and CE (Table 2), we observed the lowest CE at a low frequency of nitrogen, while the highest CE was apparent at the highest frequency of nitrogen (Figure 5A). Moreover, the CE was negative under the combination of low pressure and a low frequency of nitrogen addition (Figure 5A). The CE was observed at the maximum value, and a t-test indicated that it was significantly greater than 0 under the combination of high pressure and a high frequency of nitrogen addition (Figure 5A).

**Discussion**

**Effects of the frequencies of nitrogen addition and propagule pressure on S. canadensis**

Increasing the propagule number promoted the invasion of S. canadensis by significantly increasing its growth and RDI (Figures 2 and 5). Our finding coincides with other research that has shown that increasing the propagule pressure may be crucial at enhancing the invasion of exotic clonal plants (Lockwood, Cassey, and Blackburn 2019; Simberloff 2009; Liu, Chen, and Dong et al. 2014; Liu, Sun, and Müller-Schärer et al. 2016; Blackburn, Lockwood, and Cassey 2015; Enders, Havemann, and Ruland et al. 2020). High propagule pressure sometimes increased the biomass of whole plant population at the expense of the reduced growth of individual plants (Liu, Chen, and Dong et al. 2014; Barney et al., 2016; Ren, Yang, and Li et al., 2020). However, our results showed that the growth of individual S. canadensis was not inhibited (Fig. 51). This could be attributed to the low density of invasion species (Lockwood, Cassey, and Blackburn 2019).

In contrast, there were no significant effects on S. canadensis growth and RDI under different frequencies of nitrogen, which addresses the second question of this study. It is known that many factors can determine how nitrogen addition affects plant growth, including the capability of species, season, stage of plant development, and soil moisture (Waller, Allen, and Barratt 2020; Lamb, Stewart and Cahill 2012). Some plants with a robust tolerance to environmental stress are not sensitive to changes in the frequency of nitrogen addition (Grime 1994). Thus, S. canadensis, which is strongly adaptable to different ecosystems, may respond weakly to varying frequencies of nitrogen addition. More notably, S. canadensis, as an invasive plant, has greater plasticity and is better able to adapt to different resources, so it has different strategies to adapt to varying frequencies of nitrogen addition (Lamb, Stewart and Cahill 2012). Therefore, in this study, a frequency of high nitrogen helped the growth of S. canadensis to some extent, and a high propagule pressure more significantly promoted the growth and RDI of S. canadensis under high frequencies of nitrogen addition, thus, accelerating the invasion of S. canadensis. This answered the third question and
is consistent with the findings of previous studies (Lockwood, Cassey, and Blackburn 2019; Melbourne, Cornell and Davies et al. 2007; Chun, Van Kleunen, and Dawson 2010).

**Effects of the frequencies of nitrogen addition and propagule pressure on native communities**

At the functional group level, the aboveground and total biomass of the legumes decreased significantly with the increase in propagule pressure, while all the remaining biomasses did not respond (Figures 3 and 4). This suggested that legumes could not gain a fitness advantage in mixtures with grasses and forbs (Li, S, and Liu et al. 2021; Jensen, Carlsson, and Haugaard-Nielsen 2020; He, Montesinos, and Thelen et al. 2012). At the community level, propagule pressure did not affect the biomass of community. One possible explanation is that invasion by *S. canadensis* into plant native communities requires a longer term than that used in this experiment (Hess, Buisson, and Jaunatre et al. 2020; Catford, Smith, and Wragg et al. 2019). Furthermore, as the dominant functional group, grasses did not respond to the propagule pressure; therefore, the whole community did not respond either, which is consistent with the findings of previous studies (Phoenix, Johnson, and Grime et al. 2008).

In addition, the biomass of three functional groups did not significantly respond to different frequencies of nitrogen addition, which is consistent with previous studies (Temperton, Mwangi, and Scherer-Lorenzen 2007; Rojas-Botero, Kollmann, and Teixeira 2021). As for the community level, the biomass of invaded community increased under a low frequency of nitrogen addition.
addition, while this decreased under a high frequency of nitrogen. Our findings are consistent with those of previous studies (Britton and Fisher 2007; Hwang and Lauenroth 2008). Overall, the efficiency of native plants at utilizing resources is lower than that of invasive plants, and they are more adaptable to the original low level of nitrogen. Therefore, the nitrogen utilization efficiency of native plants and invasive plants are similar at low levels of nitrogen, while a high level of nitrogen is more advantageous to the utilization of nitrogen by invasive plants, which is not advantageous to the growth of native plant communities (He, Montesinos, and Thelen et al. 2012).

Moreover, the low frequency of nitrogen addition decreased the CE of S. canadensis on the native communities, and the CE was negative under the combination of a low frequency of nitrogen addition and low propagule pressure. This indicated that the competition between S. canadensis and local communities weakened under a low frequency of nitrogen addition,
Figure 4. Effects of the frequency of nitrogen addition and propagule pressure on biomass (mean ± SE, n = 6) of each functional group: legumes (A, D, G); grasses (B, E, H); forbs (C, F, I). Different capital letters indicate significant differences among propagule pressure, and lowercase letters indicate significant differences among the frequency of nitrogen addition.

Table 2. Summary of ANOVAs for the effects of nitrogen addition frequency (N) and propagule pressure (P) on the competitive effect (CE) and relative dominance index (RDI) of Solidago canadensis.

|         | N     | P     | P     | N×P   |
|---------|-------|-------|-------|-------|
|         | F_{5,10} | P     | F_{5,10} | P     | F_{5,10} | P     |
| CE      | 1.48   | 0.243 | 0.52   | 0.477 | 0.09     | 0.918 |
| RDI *   | 2.22   | 0.126 | 14.46  | 0.001 | 0.03     | 0.973 |

*indicates square root-transformed data. Significant values of F and P are shown in bold. ANOVA, analysis of variance.

Figure 5. Effects of the frequency of nitrogen addition and propagule pressure on the competitive (A) and relative dominance index (B) (mean ± SE) of Solidago canadensis. Different capital letters indicate significant differences among propagule pressure, and lowercase letters indicate significant differences among the frequency of nitrogen addition.
which can help the native communities to resist invasion (Price and Pärtel 2013), weakening the competitiveness of *S. canadensis*.

**Conclusion**

The results of this study showed that propagule pressure significantly increased the growth and relative dominance index of *S. canadensis* and decreased the aboveground and total biomass of legumes. Compared with a high frequency of nitrogen addition, the total and belowground biomass of the native plant communities increased under a low frequency of nitrogen treatment. In summary, high propagule pressure favors the successful invasion and development in the *S. canadensis*, while a low frequency of nitrogen is beneficial to the growth of local community and helped them to resist invasion. This study helps us to understand the role of propagule pressure and frequency of nitrogen addition on the successful invasion of exotic plant *S. canadensis*. However, our experimental design limited our ability to explore the allelopathy of *S. canadensis*, and further experiments are needed to test how their allelopathy affects native communities during the density-frequency experiment. To fully explain how nitrogen deposition affects alien plant invasion, it is essential to conduct more long-term studies, including those in the field.

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**Disclosure statement**

No potential conflict of interest was reported by the author(s).

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**Data availability statement**

The data that support the findings of this study are available from the corresponding author, Hong-Li Li, upon reasonable request.

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