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# Warming and elevated nitrogen deposition accelerate the invasion process of *Solidago canadensis* L.

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## Abstract

**Background:** Invasive species can threaten native diversity and alter ecosystem processes while interacting with other components of global environmental change. Invasive plants are becoming increasingly problematic and this can be stimulated by changes in the environment. However, existing studies have primarily investigated the effects of environmental change on a specific stage of plant invasion rather than the continuous invasion process.

**Methods:** A space-for-time substitution experiment was performed to investigate how warming and nitrogen deposition affects the invasion process of a plant. Specifically, different ratios of invasive *Solidago canadensis* L. to native *Artemisia argyi* Levl. et Van were employed as a proxy to represent successive levels of invasion. A total of seven treatments were applied in the experiment: ambient (CK), N addition (+5, +12 g $m^{-2}$ $year^{-1}$), warming (+1.15, +1.86 °C) and their interaction (5 g N $m^{-2}$ $year^{-1}$ + 1.15 °C, 12 g N $m^{-2}$ $year^{-1}$ + 1.86 °C). The growth performance and competitiveness of *S. canadensis* were investigated.

**Results:** The competitiveness of *Solidago canadensis* decreased linearly with its invasion degree ($p < 0.05$). Non-linear regression showed that *S. canadensis* invasion levels of 53%, 53%, 68%, 55% and 58% were the critical thresholds for shifting the direction or magnitude of chlorophyll, leaf nitrogen, leaf shape index, diameter, and root/shoot ratio, respectively. Compared with the ambient treatment (CK, no warming and no N addition), the diameter, height, biomass and relative competitiveness of *S. canadensis* were each limited by warming, to a certain extent, whereas these and the above parameters were significantly increased by nitrogen deposition. The interaction of increased temperature and nitrogen deposition led to significant increases in the growth and competitiveness of *S. canadensis*, and this effect was detected in every stage of the invasion, throughout the invasion process.

**Conclusions:** Environmental change might have a continuous, progressive, and augmentative effect on the phenotypic traits of *S. canadensis*. This study provides fairly robust evidence that environmental change promotes the invasion process of *S. canadensis* in general, not simply in specific stages. In the future, rather than focusing on specific stages, experimental studies should consider examining invasion on a broader scale.

**Keywords:** Environmental change, Phenotypic trait, Competitiveness, *Solidago canadensis* L., Invasion process

## Introduction

Exotic invasive species are garnering much attention, because they can severely damage and impair the structure and functioning of native ecosystems, disrupt key ecological processes, affect agricultural production, and even cause huge economic losses worldwide (Diagne

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et al. 2021). A species is considered invasive when it is spreading beyond its natural area of distribution (Wang et al. 2017a). After successfully passing through the introduction, colonization, and establishment phases, a species finally achieves invasiveness and is often expanding its range size exponentially (invasive phase) (Dai et al. 2020). Thus, the invasive process of an alien species may be one that is out of control, marked by runaway population growth (Ren et al. 2019), for which the spreading stage contains different invasion degrees, which can reflects the invader's status in a region. Given that invasive species are likely to invade continuously and some of them would persist, it is expected that the degree of invasion will increase almost constantly, unless management activities can act to slow or even reverse this pattern (Guo et al. 2015). For this reason, the plant invasion process has been considered an increase from a small to large quantity of an invasive species, with its role enhanced from minor to major in a specific region and/or community (Guo et al. 2015; Zhang et al. 2020). In other words, the invasion process refers to a continuous and/or dynamic expansion process, one consisting of innumerable successive invasion degrees (ranging from 0 to 100%).

Invasion degree is a static term, referring to the status of invasion, which can be obtained by measuring the extent to which a community has already been invaded. This degree can be expressed as different numbers of exotic species or different ratios of invasive to native plants, for indicating the fractions of invaded species richness and biomass at the population or community level (Fenouillas et al. 2021). However, existing studies of plant invasion have merely investigated three stages of invasion: (1) monoculture of a native species (i.e., no invasion); (2) native and invasive plants mixed in the habitat (usually at equal proportions); as well as (3) monoculture of an invasive species (i.e., invader monoculture) (Lazzaro et al. 2014; Ren et al. 2020a). Furthermore, most studies have focused on community invisibility (i.e., soil and native species properties) after the invasion has occurred (Cheng et al. 2021b; Dyderski and Jagodziński 2019). By contrast, we know far less about processes determining the alien plants' quantity, in going from few to many, and their shift from a minor to major role in a community, including the invasiveness (i.e., performance and competitive strategy) dynamics of invasive species at different degrees of invasion. For these reasons, the identification of critical invasion traits of plants, according to which their invasion is separated into stages, has been hindered.

Biological invasions are considered a global consequence of an increasingly connected world, environmental change and an increasing human population (Pyšek et al. 2020; Weldemariam and Dejene 2021). Moreover, biological invasion is reportedly a prominent component of global environmental change while also acting synergistically with its other elements (e.g., global warming, increases in nitrogen (N) deposition and atmospheric carbon dioxide, as well as land-use change) (Dukes and Mooney 1999; Ren et al. 2021b; Theoharides and Dukes 2007). As recently reported, numerous invasive species share traits enabling them to capitalize upon a wide variety of elements under global change. Thus, invasive plants often benefit more from global environmental change than do native plants, i.e., environmental change promotes plant invasion (Liu et al. 2017; Parepa et al. 2013). However, the above findings, based on particular physiological or growth traits in the field or a greenhouse experiment at one site may be difficult to extrapolate to other sites or invasion stages (Zhang et al. 2020). Considering that most observations are specific to a time, invasion degree, place and spatial scale, along with separating the integral process of invasion (Theoharides and Dukes 2007), this may result in cognitive biases in plant invasion knowledge and prediction.

According to several recent studies, the effects of the invaders with different invasion degrees on plant taxonomic diversity and their performance traits vis-à-vis native species together plays an important role in the mechanisms of successful plant invasion (Fenouillas et al. 2021; Wang et al. 2019). Yet, few studies have linked the process of plant invasion to environmental change. In fact, plant invasion refers to a continuous process, and different degrees of invasion in one site are often subject to environmental change at the same time or spatiotemporal sequences (Theoharides and Dukes 2007). Thus, understanding the effects of environmental change on the plant invasion process (i.e., different invasion degrees), rather than the specific invasion stage, is imperative to better understand the correlation between environmental change and plant invasion.

Temperature and nitrogen are limiting factors for plant performance and are strongly impacted by anthropogenic environmental change (Ren et al. 2021b). Fang et al. (2021) have argued that climate change is the most critical variable affecting the spread of alien plant invasions. Climate warming can generally affect plant performance by changing source–sink relationships and thermal requirements of species. Therefore, global warming may facilitate the invasion of alien species from warmer ranges into a region, where it is otherwise too cold for an invader to compete with native species (Peng et al. 2019). Atmospheric N deposition is estimated to increase by 2–3 times during the twenty-first century (Yang et al. 2021), which can affect plant performance by changing both their N supply and relative content of phytohormones. Increasing evidence now supports the view that nutrient enrichment is occurring, which may favor the fitness of invasive species over native species (Uddin and Robinson 2018). Moreover, climate warming is known to increase nutrient availability by promoting soil organic mineralization and increasing plants' photosynthetic activity (Ma et al. 2011). In several cases, climate warming and N deposition could jointly be responsible for successful invasions by plants (Lu et al. 2015; Song et al. 2021). In this respect, work by Peng et al. (2019) and Ren et al. (2021b) suggests that the interactive effect arising from climate warming and nitrogen deposition could render certain microhabitats more favorable to the growth of invasive species growth. Therefore, a hypothesis is proposed that environmental change promotes the invasion process of *Solidago canadensis* L. in general, not just at specific stages.

## Materials and methods

Time displacement experiments were performed to imitate the invasion process of *S. canadensis* under global warming and nitrogen deposition. The experiment was conducted in the glasshouse located at Jiangsu University, in Zhenjiang, China. The study area is characterized by subtropical monsoon climate, having an annual mean temperature of 15.9 °C, an annual precipitation of 1101.4 mm, and 1996.8 h of sunshine yearly. In particular, Zhenjiang is located at the intersection of the middle and lower reaches of the Yangtze River and the southeast coast of China, where *S. canadensis* is currently most widely distributed (Ren et al. 2020b).

### Studied species

The experiment was performed using the invasive *S. canadensis* (S) and the native *Artemisia argyi* Levl. et Van (A), both of which belong to the Asteraceae family, and are rhizomatous perennial species and complex high-stemmed plants; crucially, they have a co-occurring geographic distribution across China (Ren et al. 2020a).

*Solidago canadensis* is a wind-pollinated perennial grass whose shoots can reach 2.5 m tall, its adults form an extensive system of rhizomes and can produce over 20 000 seeds (Ren et al. 2019). Native to North America, *S. canadensis* was first introduced to Shanghai in 1935 for ornamental purposes, and since then it has been extensively distributed over 20 000 acres along the southeast coast and across the Yangtze River Basin (Qi et al. 2022). It has become a noxious invader, whose presence has led to substantial reductions in plant diversity and stability, now also seriously affecting agricultural production in the invaded regions (Wang et al. 2019; Zubek et al. 2020).

*Artemisia argyi* Levl. et Van is a native herb widespread in temperate and subtropical regions of the Northern Hemisphere. It can germinate and grow in various ecosystems and plant communities (e.g., lakes or rivers banks, mountains, urban areas) (Sîrbu and Oprea 2011). In traditional medicine, *A. argyi* is widely employed for treating diabetes, and whole plant extracts are used for treating epilepsy in China (Li et al. 2018).

### Plant cultivation

The seeds of *S. canadensis* and the native *A. argyi* were collected from a suburb and planted in the greenhouse of Jiangsu University (32°13′N, 119°28′E). When germinating seeds grow to a height of about 1 cm, they can be diluted to the required number of plants to achieve a mixed culture treatment (Xiong et al. 2016). Different ratios of *S. canadensis* (S) to *A. argyi* (A) were used as a proxy to represent successive levels of invasion (Ren et al. 2021a). A total of six invasion degrees scenarios were set up: (**I1**) the early stage of the invasion, consisting of one seedling of *S. canadensis* with three seedlings of *A. argyi* (S1A3: 25% invader relative density); (**I2**) below the intermediate stage of the invasion, in which there were two seedlings of *S. canadensis* and three seedlings of *A. argyi* (S2A3: 40% invader relative density); (**I3**) the intermediate stage of the invasion, consisting of three seedlings of *S. canadensis* as well as three seedlings of *A. argyi* (S3A3: 50% invader relative density); (**I4**) above the intermediate stage of the invasion, in which there were three seedlings of *S. canadensis* and two seedlings of *A. argyi* (S3A2: 60% invader relative density); (**I5**) the dominant stage of the invasion, consisting of three seedlings of *S. canadensis* but just one seedling of *A. argyi* (S3A1: 75% invader relative density); (**I6**) displacement of native species, consisting only of three seedlings of *S. canadensis* (S3A0: 100% invader relative density) (Fig. 1). The individual seeding of *S. canadensis* was also planted in pots during the experiment for calculating the competitiveness. The total number of seedlings was grown in each pot according to the founder effect in genetic drift and the absolute and relative density of the target species (Barrett et al. 2008; Brooks and Crowe 2018; Flanagan et al. 2021). Each cultivation treatment was set up in 70 replicates, and the pots were randomly arranged in the greenhouse under natural lighting. Any rare weeds that emerged in the pots spontaneously were removed by hand during course of the experiment.

### N deposition and warming treatments

The N deposition levels used in this experiment were set to 5 g $m^{-2}$ $year^{-1}$ (N5) and 12 g $m^{-2}$ $year^{-1}$ (N12), to mimic the level of atmospheric N deposition at the end of this century, following the differential increase in rates of N deposition expected for China (low level: 0.05 g $m^{-2}$ $year^{-1}$ versus a high level 0.12 g $m^{-2}$ $year^{-1}$) of China (Liu et al. 2013; Ren et al. 2021b) (Fig. 1). The

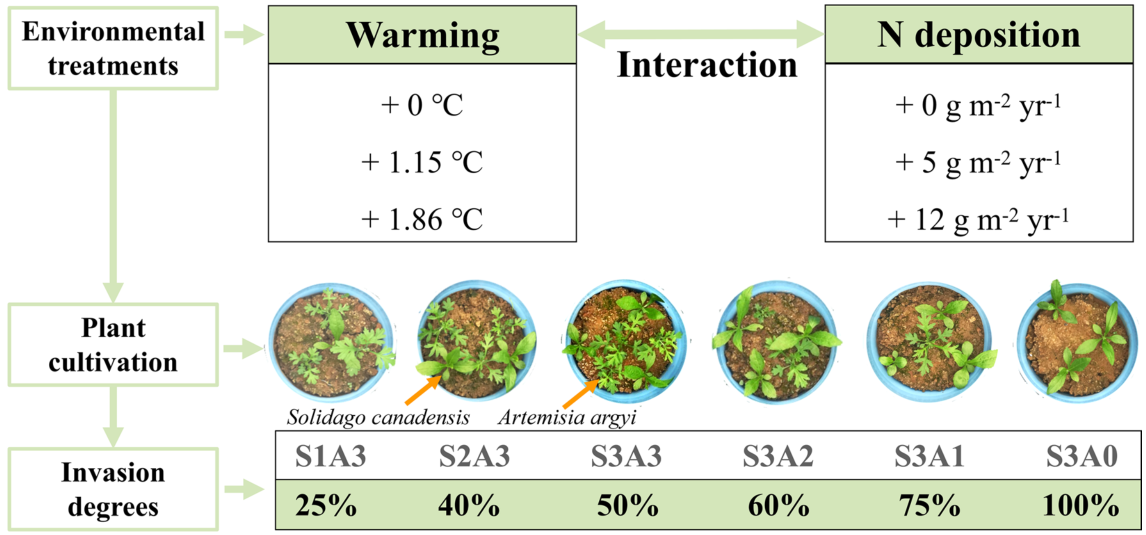

**Fig. 1** Experimental design showing: warming and elevated nitrogen deposition effect on the invasion process of *Solidago canadensis* L.

greenhouse was partitioned into two compartments, to simulate a warming gradient, this generated by in-house ventilators (380 V, 2000 W). In one compartment, two ventilators were opened, as T1 (Dannehl et al. 2012; Willits 2003), and in the other compartment the ventilators remained closed, as T2 (He et al. 2011). The control group was located near the greenhouse with a roof equipped with a solar panel (CK). During the study period, the mean temperature in T1 and T2 reached 30.62 ± 0.36 °C and 31.33 ± 0.37 °C, respectively, this being 1.15 °C and 1.86 °C higher than 29.47 ± 0.38 in the control group, respectively ($p < 0.05$). Both increases successfully mimicked the projected global warming by 2050 (Rogelj et al. 2012) (Fig. 1).

Thus, a total of seven treatments were applied in the experiment, which included two combinations of treatments: CK, N5, N12, T1, T1N5, T2, T2N12. A total of 490 pots were thus used ([6 invasion degrees + 1 monoculture] × 7 environmental treatments × 10 replicate pots), these randomly moved around every week to reduce position-bias effects (Du et al. 2017), to simulate environmental change acting upon the plant invasion process.

### Plant parameters measured

Based on the above-described treatment conditions, the plants were destructively harvested after 83 days of exposure to warming and N deposition. Leaf nitrogen content and chlorophyll were measured using a portable chlorophyll meter (TYS-A, TOP, Zhejiang, China) before the final harvest (Xi et al. 2019). Leaf shape index (LSI) was calculated as the ratio of leaf length to the corresponding leaf width (Wang et al. 2016). One plant from each pot was randomly selected to measure plant height, basal diameter and the total biomass obtained after oven-drying the plant. The root/shoot ratio was calculated as the ratio between the root biomass and the shoot biomass (Wan et al. 2019).

To evaluate competition between *S. canadensis* (S) and *A. argyi* (A) under environmental change, the relative yields (*RY*) for *S. canadensis* was calculated according to Garcia-Serrano et al. (2007) by using this formulae: $RY = Y_{SA}/(p \times Y_S)$, where $Y_S$ denotes the yield (total biomass) of S in monoculture, $Y_{SA}$ denotes the yield of S when grown with A, and $p$ is expresses the initial proportion of species S and A in their mixed setting. An $RY > 1$ implies S is a superior competitor to A, conversely, an $RY < 1$ implies S is an inferior competitor to A, in the event of $RY = 1$, then species S has an equal competitive ability with species A. The higher the value of *RY*, the stronger the inferred competitiveness would be. Because this study aimed to explore the invasion process under environmental change, the *RY* of *A. argyi* was not calculated and presented here (Wu et al. 2017).

### Statistical analyses

A three-way ANOVA (analysis of variance) was used to simultaneously test the effects of invasion degree (I1-6; six levels), temperature (two levels), N deposition (two levels) and their interactions on the variation in parameters of *S. canadensis*. Tukey's post-hoc pairwise comparison tests was used at $\alpha = 0.05$ for significance to distinguish difference in means between treatments. Linear regression models were fitted to determine the effect of invasion degree upon each growth parameters as well as on the competitiveness of *S. canadensis*, data that did not fit a linear regression model (non-linear response to invasion levels) were analyzed in-depth using locally estimated scatterplot smoothing (LOESS) regression, connected by modified Bezier curve, for which statistical significance was estimated using the overlap rule for SE bars (Cumming et al. 2007; Zhang et al. 2020). All statistical analyses were implemented in SPSS software (v22, 2013 IBM). All figures were drawn using OriginPro 8.6 software (Originlab Co., Northampton, MA, USA).

## Results

All phenotypic traits of *S. canadensis* were significantly affected by nitrogen and temperature ($p < 0.05$, Table 1), whereas the root/shoot ratio and the competitiveness were not affected by temperature. The invasion level significantly affected diameter, height, biomass and competitiveness, whereas it did not affect chlorophyll, leaf nitrogen, leaf shape index, as well as root/shoot ratio. There were no significant three-way (warming, N and invasion degree) interactions detected for the phenotypic traits of *S. canadensis* ($p > 0.05$, Table 1). However, the effect arising from N on chlorophyll, leaf nitrogen and biomass was changed by temperature and invasion level, respectively (lower order, two-way interactions, $p < 0.01$, Table 1). Furthermore, the interaction between nitrogen and temperature significantly affected root/shoot ratio and competitiveness of *S. canadensis* ($p < 0.05$, Table 1).

### Phenotypic changes in *S. canadensis* during its the invasion

Ecological phenotype varied with the invasion degree of *S. canadensis*, as evinced by changes in this plant's chlorophyll, leaf nitrogen, leaf shape index, diameter, height and biomass, as well as its root/shoot ratio and relative yield (Fig. 2). The invasion level (i.e., increasing invader relative ratios) was positively correlated with biomass in a linear manner ($r^2 = 0.96$, $p = 0.03$) but negatively so with relative yield ($r^2 = 0.68$, $p < 0.01$) (Fig. 2g, e). However, most phenotypic parameters showed non-linear responses to increasing invasion levels. Chlorophyll and leaf nitrogen remained stable or slightly reduced as the invasion level approached 53%, after which they rose (Fig. 2a, b). Diameter ($p < 0.01$) decreased at a 55% invasion level, but then increased with *S. canadensis* invasion levels, reaching values similar to or higher than those of the early invasion stage (Fig. 2d). There was no significant linear correlation between plant height and invasion degree. By contrast, height at the 50% invasion level was significantly lower than that at the 25%, 40% or 100% invasion levels (Fig. 2e). There were no significant differences in chlorophyll, leaf nitrogen, leaf shape index and root/shoot ratio among the invasion levels (Fig. 2a–c, g). According to the non-linear regression results, invasion levels of 53%, 53%, 68% and 55% corresponded to critical thresholds for chlorophyll, leaf nitrogen, leaf shape index and diameter, respectively, at which the parameters significantly shifted in direction or magnitude (Fig. 2a–d, g). For the root/shoot ratio, not one but three of the critical inflection points were apparent at an invasion degree of 27%, 58% and 80%, respectively (Fig. 2g).

### Effects of changing temperature and nitrogen supply on the growth and competitiveness of *S. canadensis*

Compared with normal growing conditions (i.e., the control), chlorophyll and leaf nitrogen in *S. canadensis* were noticeably higher in all other treatments (Fig. 3a, b). The leaf shape index of *S. canadensis* in the T1, T1N5 and T2 treatments were significantly lower than that in the control (CK) or in N5, N12 and T2N12 (Fig. 3c). The height, stem and biomass of *S. canadensis* changed slightly in response to temperature, yet they were increased markedly by the N addition alone and the latter's interaction with temperature. The root/shoot ratio of *S. canadensis* in the N5 treatment was significantly higher than in all other treatments (Fig. 3d–f). The competitiveness of *S.*

**Table 1** Results of a three-way analysis of variance (ANOVA) testing for effects of nitrogen (*N*), temperature (*T*) and invasion degree (*I*) on phenotypic traits of *Solidago canadensis*

| Traits | Nitrogen (*N*) | Temperature (*T*) | Invasion (*I*) | *N* × *T* | *N* × *I* | *T* × *I* | *N* × *T* × *I* |
|---|---|---|---|---|---|---|---|
| Chlorophyll | 187.46** | 80.185** | 0.456 | 8.82** | 3.34** | 1.47 | 1.41 |
| LN | 194.55** | 84.42** | 0.489 | 8.66** | 3.77** | 1.57 | 1.43 |
| LSI | 5.67** | 13.35** | 1.242 | 2.54 | 0.83 | 1.2 | 1.31 |
| Diameter | 160.14** | 7.39** | 12.04** | 0.44 | 1.26 | 0.92 | 0.89 |
| Height | 142.96** | 14.54** | 3.58** | 0.33 | 0.91 | 1.44 | 1.04 |
| Biomass | 167.55** | 18.84** | 56.88** | 11.92** | 2.43** | 1.61 | 1.08 |
| RS | 3.33* | 2.91 | 0.898 | 4.34* | 1.06 | 0.4 | 0.91 |
| RY | 11.85** | 1.37 | 4.71** | 5.06** | 0.85 | 0.82 | 0.62 |

* and ** indicate $p < 0.05$ and $p < 0.01$, respectively. LSI, LN, RS and RY indicate leaf shape index, leaf nitrogen, root/shoot ratio and relative yield, respectively

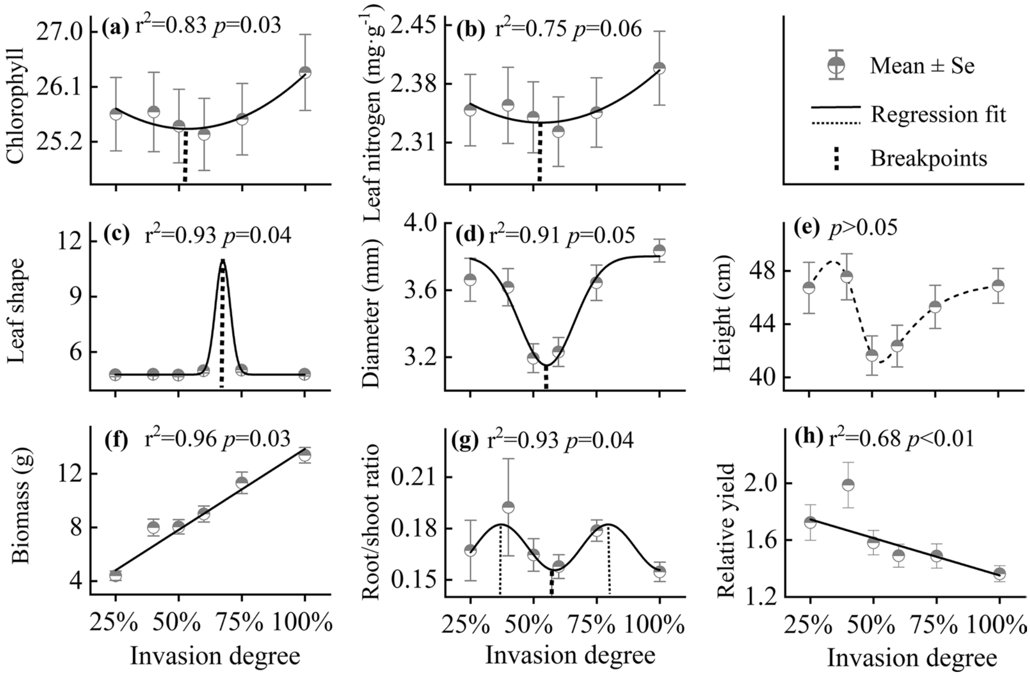

**Fig. 2** Growth and changed competitiveness of *Solidago canadensis* at differing degrees of invasion. Ecological traits show different patterns of response to the gradient of invasion (25–100% invasion levels), which displayed linear or non-linear relationships. Solid lines represent significant linear or non-linear fits, dashed lines represent non-significant linear or non-linear fits, and vertical dotted lines indicate the breakpoints identified via piecewise regressions. Error bars represent the SEs of the means (N = 70)

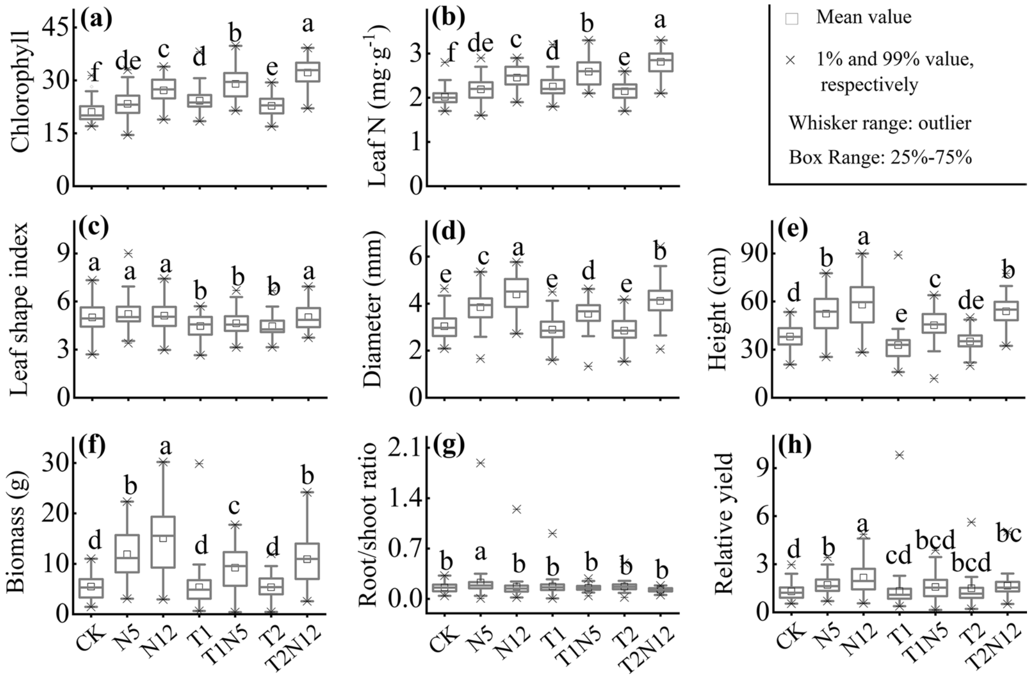

**Fig. 3** Responses of growth and competitiveness of *Solidago canadensis* to environmental change. A total of seven environmental treatments were imposed: CK (control), N5 (N addition 5 g m$^{-2}$ yr$^{-1}$), N12 (N addition 12 g m$^{-2}$ yr$^{-1}$), T1 (temperature increase of 1.15 °C), T1N5 (combined 1.15 °C temperature increase and N addition of 5 g m$^{-2}$ yr$^{-1}$), T2 (temperature increase of 1.86 °C) and T2N12 (combined 1.86 °C temperature increase and N addition of 12 g m$^{-2}$ yr$^{-1}$). The sample size for each group in each boxplot is 60

*canadensis* was significantly stronger in the N5, N12 and T1N12 treatments than the control (Fig. 3h).

### Effects of temperature and nitrogen changes on the invasion process of *S. canadensis*

The chlorophyll and leaf nitrogen of *S. canadensis* each fluctuated only slightly across the six invasion stages, whereas they were significantly affected by environmental change. During the invasion process, compared with the control, both chlorophyll and leaf nitrogen of *S. canadensis* in the N12, T1, T1N5, and T2N12 treatments were significantly higher ($p < 0.05$, Fig. 4a, b). At the same time, environmental change had an insignificant effect on the leaf shape index and root/shoot ratio of *S. canadensis* ($p > 0.05$, Fig. 4c, g). For diameter, its trend of change was similar to that of height, in that it was significantly lower in the control treatment than the N5, N12, T1N5 and T2N12 treatments, yet higher than either the T1 or T2 treatments to a certain extent (Fig. 4d, e). Except for the T1 treatment, the competitiveness of *S. canadensis* was greater in the environmental treatments than the control (CK) throughout the invasion process, for which some differences attained statistical significance (Fig. 4g). Notably, the competitiveness of *S. canadensis* was negative and linearly correlated with the degree of invasion under the N5, N12 and T2N12 treatments ($p < 0.05$), whereas its biomass was correlated in a linear, positive manner with invasion level (all $r^2 \geq 0.80$, $p < 0.05$). The N addition alone and its interaction with warming both had a significant, prompt effect on the biomass of *S. canadensis* when compared with control and warming-alone treatments across the six-stage invasion process (Fig. 4f).

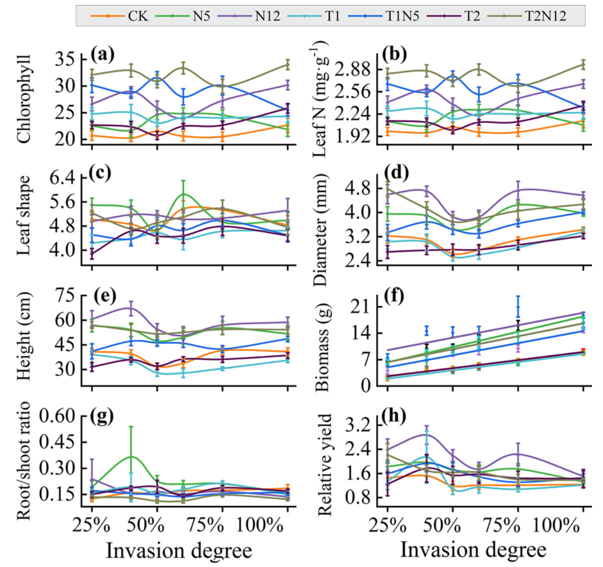

**Fig. 4** Effects of environmental change on the invasion process of *Solidago canadensis*. Linear regression models were fitted to determine the effect of invasion degree on growth parameters as well as on the competitiveness of *S. canadensis*. Data that did not fit a linear regression model (non-linear response to invasion levels) were analyzed using locally estimated scatterplot smoothing (LOESS) regression, and connected by modified Bezier curve. A total of seven environmental treatments were imposed: CK (control), N5 (N addition 5 g m$^{-2}$ yr$^{-1}$), N12 (N addition 12 g m$^{-2}$ yr$^{-1}$), T1 (temperature increase of 1.15 °C), T1N5 (combined 1.15 °C temperature increase and N addition of 5 g m$^{-2}$ yr$^{-1}$), T2 (temperature increase of 1.86 °C) and T2N12 (combined 1.86 °C temperature increase and N addition of 12 g m$^{-2}$ yr$^{-1}$). Error bars represent the SEs of the means ($N$=10)

## Discussion

### Invasion level affects the phenotypic traits of *S. canadensis*

The degree of invasion can be quantified as the total number of alien plant species or their proportion of the total species richness within the invaded ecosystems (Jaunia and Hyvönen 2010). Accordingly, studies on the phenotypic traits of invasive plants mainly focus on three invasion stages (0, 50% and 100% invasion level) when comparing the performance of plant species during the invasion process (Cheng et al. 2021b; Jauni et al. 2012; Lau and Suwa 2016; Li et al. 2017; Ortmans et al. 2016; Wang et al. 2019). In this study, we focused on the performance of *S. canadensis* and its linear response to invasion level, even deducing those critical invasion thresholds, where plant traits responded non-linearly to the invasion process.

As the ratio of the invasive weed *S. canadensis* to the native *A. argyi* is increased, it generated differential changes in the former's traits characterized by linear and non-linearly responses. In some cases, the non-linear responses featured clear thresholds, where given parameters of interest changed dramatically in magnitude and/or direction. Although multiple inflection points were found for the root/shoot ratio, this parameter was not significantly changed by invasion level. This suggests the root/shoot ratio of *S. canadensis* was stable, but liable to several small fluctuations under different invasion levels. A significant shift in the response of phenotypic traits was identified when the invasion degree ranged from 53% to 68%. This is consistent with work by Zhang et al. (2020), who found a pronounced shift in the response of soil parameters (i.e., ammonium nitrogen, SOM and catalase) when the ratio of the invasive *Conyza canadensis* to *Lactuca sativa* spanned 47–69%. The threshold at a particular invasion level may represent a vital event during the invasion process, which would support the concept of 'threshold of potential concern' (TPC): that is, the species beyond this stage can reduce some barriers that hinder their invasion, such that a smaller subset become transformer weeds (Foxcroft 2009). The above findings suggest that an invasive species, especially once it has reached an invasion level higher than 50% as in the case of *S. canadensis*, could undergo major changes in its physiological, growth and allocation strategies with potential downstream effects on its invasion, thus probably facilitating the spread and dominance of it and perhaps other alien species into natural communities. In this study, invasion levels significantly affected stem-related traits but did not leaf-related traits. The height and diameter performance of *S. canadensis* was worst at the 50–60% invasion stage, probably due to peak plant density (S3A3 and S3A2) at this stage, leaving stem growth constrained by less space and resources available (Brooks and Crowe 2018). Likewise, Cheng et al. (2021a) found that the height of *S. canadensis* changed substantially with an increasing invasion degree, while its leaf-related traits of leaf width, length, area, chlorophyll and nitrogen content did not. The above results suggest stem-related traits are more sensitive than leaf-related traits to interspecific and/or intraspecific competition, probably due to the leaf organ being capable of greater phenotypic plasticity. For instance, the leaf could try to maintain its stability and physiological balance by regulating the direction it faces, its inclination (angle) and petiole length at the different intensities of competition and/or invasion degrees (Wang et al. 2017b; Yang et al. 2011). However, the stem lacked such plasticity for overcoming competition and/or circumventing adverse density-related effects.

Besides the stem-related traits, our results also suggest the biomass and competitiveness of *S. canadensis* were significantly affected by the invasion level. This finding is contrary to the results of an existing study, Ortmans et al. (2016) who suggested that the aboveground biomass and relative competition index of the invasive plant *Ambrosia artemisiifolia* L. were similar across different invasion levels. This discrepancy between studies might be explained by two reasons. First is the residence time, in that *S. canadensis* was introduced to Shanghai (China) in 1935, but *A. artemisiifolia* was introduced to Europe in 1870 (Chauvel et al. 2006). The elapsed time from the first record in the wild until present is recognized as a vital determinant of the geographical range sizes and invasion stages of alien plant species. For instance, Hakes and Cronin (2012) suggested that phenotypes may be highly dependent on the successional-stage, which is critical to *S. altissima* invasions. Second is the definition of invasion employed, in that the spatial invasion pattern in Ortmans et al. (2016) had been derived from a pollen density map, with only three levels considered. In our study, six degrees of invasion were set up according to different ratios of the invader to native species, and their density effects also considered.

Interestingly, the competitiveness of *S. canadensis* decreased linearly with the invasion level ($p < 0.01$). Pysek et al. (2020) suggested that the high competitiveness of invasive species could be a potent driver at the early stages of their invasion process. Furthermore, the higher competitiveness of an invasive species at its initial invasion stages may compensate for its disadvantage of having a lower ratio of abundance in the local community to survival (access to the initial space, nutrients and preemption of light sources). Interspecific competition often results in the negative effect of one species upon another due to limited shared resources; for instance, Adomako et al. (2019) showed that *S. canadensis* grew worse when the diversity or density of the co-occurring residents increased. Once it has entered the phase of advanced invasion and attains high fitness in the regional community, *S. canadensis* may contribute more to augmenting its growth-related characteristics than its competitive characteristics (Catford et al. 2019). Consequently, plant biomass of the invader increased significantly with the degree of its invasion, probably because of the competition pressure released from native species at later invasion stages. Furthermore, the allelopathic effects of invasive *C. canadensis* on the seedling height, seedling biomass, germination index and vigor index of native *L. sativa* weakened with a greater degree of invasion (Wang et al. 2017a). As a co-invasive species, leaf extracts of *S. canadensis* also significantly inhibits the seed germination of native *L. sativa* (Wei et al. 2020a), but *S. canadensis* has positive allelopathic effects on its own growth (Adomako et al. 2019); hence, intraspecific competition in *S. canadensis* may be mutually beneficial. It is speculated in these studies that the more intense allelopathic effects and competitiveness of *S. canadensis* at a lower invasion degree may be coupled favoring the population growth of *S. canadensis* in ecosystems by inhibiting the seed germination and the growth of co-occurring plant species.

### Effects arising from temperature and nitrogen on the invasion process of *S. canadensis*

Environmental change is known to play an important role in the spread of biological invasions at particular invasion stages (Ren et al. 2021b; Theoharides and Dukes 2007). Recognizing the environmental factors behind alien plant success throughout the invasion process may be more meaningful than focusing solely on separate stages of invasion, which could improve our ability to explain and predict the spread of invasive species.

From the perspective of environmental change, chlorophyll and leaf nitrogen of *S. canadensis* significantly increased under warming and nitrogen deposition treatments, and a synergistic interaction was found between these two abiotic factors. This may be explained by higher temperature contributing to chlorophyll accumulation in the plant, and nitrogen addition substantially increases its leaf nitrogen concentration. Nitrogen is not only a key component of plant photosynthesis but also glucose synthesis in plants. Accordingly, augmenting both chlorophyll and nitrogen in leaves is of great significance for improving plant growth (Wei et al. 2020b). In short, temperature and nitrogen can jointly promote plant growth by increasing leaves' chlorophyll and nitrogen concentrations in tandem (Bhattarai et al. 2021).

The temperature and nitrogen interaction also had other significant synergistic effects. Compared with the control group, the diameter, height, biomass and competitiveness of *S. canadensis* plants were suppressed by warming to a certain extent yet these traits significantly benefited from nitrogen deposition. Thus, it is not surprising that the synergistic effect of warming and nitrogen addition is able to increase the success rate of *S. canadensis* invasion. Likewise, Cavieres et al. (2017) showed that the invasive plant *Poa annua* L. harbored a competitive advantage over native plants only under higher temperatures and greater nitrogen-use efficiency. Under low temperatures and low supply of soil nitrogen, native species may resist the invasion of *P. annua*. Accordingly, the interaction between temperature and nitrogen is beneficial for improving the relative competitiveness of invasive plants. By contrast, Wang et al. (2021) found that nighttime climate warming enhances the inhibitory effects of atmospheric nitrogen deposition on the success of invasive *S. canadensis* vis-à-vis native species. Hence, multiple plant species with different life histories should be selected when conducting such invasion experiments.

Several studies have demonstrated that phenotypic traits of invasive species can change with the environment and/or invasion stage (Cheng et al. 2021a; Uddin and Robinson 2018; Verlinden et al. 2014; Zhang et al. 2020), but how the invasion process changes with the environment remains understudied. Here, we performed a direct test of the impact of environmental change upon the performance and competitiveness of *S. canadensis*, under different degrees of invasion, to reveal how environmental change affects the invasion process of *S. canadensis*. Moreover, to our best knowledge, this is the first experimental test of environmental change that is presumed to play a key role in the invasion process. We show that environmental variables explaining the invasion success of the species do change at respective invasion stages, but we also find that they figure prominently throughout the invasion process (Fig. 4). Specifically, when compared with the control, the growth and competitiveness of *S. canadensis* increased considerably with the nitrogen addition alone and its interaction with climate warming across the invasion process. This strongly supports our hypothesis of environmental change promoting the invasion process of *S. canadensis* in general, not just specific stages. These results are also partly in line with those of Wu et al. (2017), Ren et al. (2021b), Verlinden et al. (2014) and Cavieres et al. (2017), who all found that nitrogen addition, climate warming and their interaction augmented the biomass and competitiveness of invasive species at a specific stage. Their explanation for these results was that soil N availability and thermal regimes were changed by nitrogen deposition and climate warming, respectively. In future research, the invasion process instead of certain stages should be explicitly considered in plant experiments, because although different stages together constitute an entire process they cannot substitute for it.

## Conclusions

This study revealed that an invasion degree of around 55% could represent a critical invasion threshold for *S. canadensis*. The identification of critical invasion thresholds is considered a key step toward mitigating effects of invasive plants on biodiversity. In addition, the competitiveness of *S. canadensis* was negatively and linearly related to invasion degree, probably due to release of competition pressure from co-occurring native species as the invasion process advanced and strengthened. Climate warming and nitrogen deposition significantly enhanced the performance and competitiveness of *S. canadensis* across all six stages of the invasion process, suggesting that such environmental changes may increase the invasiveness of this plant species. Accordingly, this study provides fairly robust evidence that environmental change promotes the entire invasion process of *S. canadensis*, and not just particular stages of it. A clear and crucial message from this work is the importance of studying plant invasion across multiple stages, as the environmental drivers relevant for it may vary from stage to stage.

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**Author contributions**

DD and ZD designed the experiment. GR and BY performed the experiment. MC and YX collected the data. GL and JL analyzed the data. GR and HZ wrote the manuscript. QJ polished the language. All authors contributed critically to the drafts and gave final approval for publication. All authors read and approved the final manuscript.

### Availability of data and materials
The data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

### Ethics approval and consent to participate
Not applicable.

### Consent for publication
Not applicable.

### Competing interests
The authors declare that they have no competing interests.

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