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Warming, nitrogen addition, and provenance regulate responses of plant leaf and stem traits of Solidago canadensis to rhizosphere edaphic properties

Jingji Li
Jianxin Ren
Juanjuan Li
Peihao Peng
Xiaohui Zhou
xiaohuizhou@cdut.edu.cn

Chengdu University of Technology https://orcid.org/0009-0008-7325-7508

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Abstract

Background and Aims

Warming and nitrogen (N) deposition modify functional traits of invasive plants and soil environments, yet mechanisms underlying how their long-term interactions shape invasive plant–edaphic relationships remain poorly understood.

Methods

We selected *Solidago canadensis* from native and invasive provenances, conducted a 10-year warming and N addition experiment to examine their effects on the leaf traits, stem traits, and rhizosphere edaphic properties.

Results

Warming significantly increased chlorophyll content and stem diameter (SD) but decreased specific leaf area (SLA); whereas N addition had no significant effects on leaf and stem traits; invasive provenance exhibited higher SLA, plant height (H), SD and stem biomass (SB), but lower leaf dry matter content (LDMC) and plant density (PD) relative to native provenance. Warming significantly elevated soil nitrate N (NN) but decreased available potassium (AK) and moisture content (MC); N addition significantly altered AK and NN; invasive-associated soils contained more AK and MC, but less NN and soil organic matter (SOM). Soil AK was the dominant driver of plant traits variation under both warming and N addition, positively correlating with H, SD and SB, but negatively correlating with LDMC. Plant provenance regulated the relationship between LDMC and NN.

Conclusion

Overall, warming, N addition, and provenance mediate plant leaf and stem traits–edaphic properties relationships. Our results indicate that invasive *S. canadensis* display stronger adaptive capacity under climate warming, and highlighted that soil AK and NN as key regulators of leaf and stem traits variation under future climate change.

Introduction

Climate warming, atmospheric nitrogen (N) deposition, and plant invasion are among the most pressing global ecological and environmental issues. Multiple studies have predicted that mean global temperature will likely increase by approximately 2°C over the next century, a magnitude that is considered a critical threshold for ecosystem responses (Brown and Caldeira 2017; McKay et al. 2022). In China, the mean surface air temperature increased by 0.30°C per decade from 1961 to 2020,

exceeding the global average warming rate over the same period (Zhou et al. 2023). In addition, atmospheric N deposition continues to intensify globally, with a global rate of approximately 0.05–2 $g \cdot m^{-2} \cdot a^{-1}$ (Stevens et al. 2022; Zhu et al. 2025). As a global hotspot region, southern China experiences N deposition rates of about 4 $g \cdot m^{-2} \cdot a^{-1}$, far exceeding the global average (Shang et al. 2024). This exerts significant pressure on native plant diversity and ecosystem function (Borer and Stevens 2022; van der Plas et al. 2024). Plant invasions, regard as the second greatest threat to biodiversity after habitat fragmentation, can disrupt biogeochemical cycles, reduce biodiversity, accelerate ecosystem degradation, and even transform entire ecosystems (Diagne et al. 2021; Xu et al. 2022). The combined pressures of climate warming and N deposition are reshaping interspecific competition and are increasing regional susceptibility to the establishment and spread of alien plants, thereby altering invasion pathways and potential distribution ranges (Hellmann et al. 2008; Lopez et al. 2022; Ren et al. 2022a, 2022b; Yang et al. 2022).

Climate warming can influence the invasion success of alien plants through multiple pathways, including phenotypic plasticity and soil properties (Ren et al. 2022; Wang et al. 2022). Warming can directly facilitate plant growth and biomass accumulation, and invasive species owing to their high phenotypic plasticity and rapid thermal adaptation respond even exhibiting stronger positive responses (Davidson et al. 2011; Lin et al. 2010). Additionally, warming-induced changes in soil water and nutrient availability can indirectly restructure organ and whole-plant architecture, thereby promoting growth and enhancing resource-use efficiency of invasive plants (Zhou et al. 2025). Atmospheric N deposition increases soil N availability in terrestrial ecosystems, which invasive plants exploit to enhance their competitive advantage (Li et al. 2024). Concurrently, these invasive plants further modulate root and stem functional traits to promote aboveground biomass and light interception, suppressing native plants performance and strengthening their invasiveness (Xiang et al. 2024). Emerging evidence suggests that warming and N deposition may act synergistically to promote plant invasion (Ren et al. 2022a; Xu et al. 2023). Overall, climate change profoundly effects plant phenotypes, yet its regulation of plant invasion depends not only on direct effects on species but also on modification of soil environments, which further reshape plant phenotypes and invasion performance (Hines et al. 2017; Tian et al. 2022).

Soil environments strongly modulate plant functional traits and growth strategies, with divergent soil conditions shaping plant trade-off patterns between resource acquisition and utilization (Daou et al. 2021). Under high soil N, phosphorus and organic matter contents or sufficient water availability, plants generally exhibit high specific leaf area (SLA), thick stems and low leaf dry matter content (LDMC), traits consistent with a fast-growth strategy that emphasize rapid resource capture and biomass accumulation (Wright et al. 2004). Conversely, plants growing in nutrient-poor, acidic or water-limited soils frequently form thick leaves, low SLA, high LDMC and dense tissues, traits representative of a conservative strategy centered on efficient resource retention and stress-defense allocation (Driesen et al. 2021; Gong and Gao 2019; Li and Li 2025). Overall, plant functional traits are tightly coupled with soil environments, forming a strong biotic feedback relationship (De Long et al. 2023). This relationship is reflected not only in divergent plant resource-use strategies but also in species-specific responses to environmental changes. Global changes such as climate warming and nitrogen deposition can alter soil environments,

thereby reshaping accordingly plant community patterns (Speißer et al. 2022; Yang et al. 2022). Invasive plants with their high phenotypic sensitivity and plasticity to soil environment changes, can rapidly gain competitive dominance and accelerate invasion processes (Blossey and Notzold 1995; Xiang et al. 2024).

Climate warming and atmospheric N deposition can facilitate plant invasion by reshaping soil environments through distinct but potentially interacting pathways (Ren et al. 2022a, b). Warming facilitates plant invasion by altering soil microbial communities and nutrient cycling to enhances resource availability for invasive plants (Inderjit and van der Putten 2010; Yang et al. 2022). For example, experimental soil warming promoted the growth of multiple invasive plants in soils with thermal legacies, indicating that warming-induced changes in soil organisms and nutrient availability generate beneficial belowground environments (Thakur et al. 2014). Moreover, soil warming can alter plant–soil feedbacks and mycorrhizal associations, suggesting that warming-driven variations in plant performance are predominantly mediated by belowground biotic processes (De Long et al. 2023; Hassan et al. 2022; Wheeler et al. 2017). Atmospheric nitrogen deposition can also facilitate plant invasion by elevating soil nitrogen availability (Shan et al. 2018). For example, nitrogen deposition enhances photosynthesis and growth of *Erigeron annuus* and *Erigeron canadensis* via elevated inorganic nitrogen (Guan et al. 2023; Guo et al. 2023; Xiang et al. 2024). Meanwhile, nitrogen deposition inhibits the recovery of native species by altering soil biota and physicochemical conditions, thereby enhancing positive feedback to invasive plants (Cui et al. 2024; Xu et al. 2022).

Most existing studies have focused on invasive plants responses to individual global change drivers, including warming and nitrogen deposition (Ivison et al. 2025; Xiang et al. 2024), multiple global change drivers can exert interactive and non-additive effects on plant invasion, rendering single-factor studies potentially insufficient and misleading (Speißer et al. 2022; Yang et al. 2022). However, long-term experimental evidence regarding the interactive effects of biotic and abiotic factors on invasive plant–soil relationships remains limited. Therefore, we selected *Solidago canadensis* L. from two provenances as study species and conducted a long-term warming and nitro gen addition experiment to explore their effects on plant leaf and stem traits, as well as soil physicochemical traits. We proposed two hypotheses: (1) warming and plant provenance significantly affect the growth of *S. canadensis*. (2) leaf and stem traits are significantly regulated by soil properties, and plant provenance significantly modulates the associations among leaf traits, stem traits, and soil variables.

Materials and methods

Study species and site

We selected *Solidago canadensis* L. populations from two provenances: five native populations from Montana, USA (46°52'–46°53'N, 113°44'–113°46'W; SNA) and five invasive populations from Ningbo, eastern China (29°51'–29°53'N, 121°31'–123°31'E; SCN). To avoid confounding effects of ploidy, representative samples from each origin were examined using flow cytometry to confirm ploidy levels.

The experiment was conducted at Chengdu University of Technology in Sichuan, China (30.67° N, 104.06° E). The region has a subtropical humid monsoon climate with a mean annual temperature of ~ 16.1°C and mean annual precipitation of ~ 918.2 mm.

Experimental design

We employed a fully factorial design with three factors (2 × 2 × 2): plant provenance (native range vs. invasive range), warming (ambient vs. warmed) and N addition (ambient vs. N addition), with each replicated eight times (n = 8), yielding 64 pots in total (Fig. 1a). The long-term experiment was conducted in June 2012 and has been continuously maintained to date. We planted 100 seeds in an experimental pot (30 cm × 30 cm × 20 cm) filled with a 1:1 mixture of sand and loam. Both components were sieved through a 1 cm mesh and thoroughly blended. After establishment, seedlings were thinned to a standardized initial density of four individuals per mesocosm, with 10 cm spacing between neighboring plants and between plants and the pot.

Experimental warming was applied using MSR-2420 infrared radiators (Kalglo Electronics, Bethlehem, PA, USA) suspended 1.5–2.0 m above the soil surface, which provided continuous year-round warming of approximately 2°C above ambient temperature (IPCC 2023; Peng et al. 2019). Control plots were equipped with dummy frames of identical dimensions to account for potential structural and shading effects. Atmospheric nitrogen deposition was simulated by manually adding ammonium nitrate (NH_4NO_3) at an annual rate of 4 g N m^{-2} yr^{-1} (Galloway et al. 2004). Based on the pot surface area, this equals an annual N addition rate of 1.028 g NH_4NO_3 per pot. The annual N dose was applied once after seedling establishment in 2012, and it was divided into four equal applications of 0.257 g NH_4NO_3 per pot, applied at 30-day intervals from March to June in 2013. The warming and N addition treatments have been maintained continuously since 2012. A detailed description of the long-term experimental design has been reported previously (Peng et al. 2019; Zhou et al. 2021).

During the experiment (2022–2023), we watered seedlings regularly and determined 13 plant and soil traits (Fig. 1b). We measured seven plant functional traits, including chlorophyll content (Chl), specific leaf area (SLA), leaf dry matter content (LDMC), plant height (H), plant stem density (PD), stem biomass (SB), and stem diameter (SD), as well as six soil physicochemical properties, including pH, moisture content (MC), soil organic matter (SOM), available phosphorus (AP), nitrate nitrogen (NN), and available potassium (AK) (Fig. 1b). Leaf traits were measured at the peak growth stage in mid-July 2022. In each pot, three individual plants were randomly selected, and five fully expanded mature leaves at similar positions were collected per plant. Chlorophyll content was measured as SPAD values using a SPAD-502 chlorophyll meter, with three readings taken per leaf and averaged for subsequent analysis. Leaf area was determined using a LA-S leaf area scanner (Wanshen LA-S Leaf Analysis Software). Leaves were then rehydrated in water for 24 h at room temperature to obtain saturated fresh mass, oven-dried at 65°C to constant mass, and weighed to determine the leaf dry mass. Specific leaf area was calculated as leaf area divided by leaf dry mass, LDMC was calculated as the ratio of leaf oven dry mass to leaf water-saturated fresh mass (accuracy 0.0001 g, Model: FA2104). Plant height and plant stem density were

recorded every 45 days from 15 July onward, with four measurements in total. Plant height was measured using the three tallest individuals in each pot. Basal stem diameter was measured with a Vernier caliper during the final measurement on 15 January 2023. After seed maturation, stems were harvested, oven-dried at 65°C for 48 h, and weighed to quantify total stem biomass per pot.

After fruiting, 200 g of surface soil were collected from each pot to determine soil physicochemical properties (Fig. 1b). Soil pH was measured potentiometrically in a 2.5:1 water: soil suspension according to NY/T 1121.2–2006; soil moisture content was determined gravimetrically according to HJ 613–2011; briefly, fresh soil mass was recorded as W_1, and oven-dry soil mass after drying at 105°C to constant mass was recorded as W_2, soil moisture content was calculated as $MC = (W_1 - W_2) / W_2 \times 100\%$. Soil organic matter was determined by dichromate oxidation followed by titration with ferrous sulfate, using a correction factor of 1.1 according to LY/T 1237–1999. Available phosphorus was extracted with ammonium fluoride–hydrochloric acid solution and quantified colorimetrically using the molybdenum-antimony anti-colorimetric method according to NY/T 1121.7–2014. Nitrate N was measured by UV spectrophotometry at 220 and 275 nm, with correction for organic matter interference according to GB/T 32737 − 2016. Available potassium was extracted with neutral ammonium acetate and determined by flame photometry according to NY/T 889–2004.

Data analysis

The normality of data was tested using the Shapiro–Wilk test and the homogeneity of variance was tested using the Bartlett's test. We performed three-way analysis of variance (ANOVA) to test the effects of plant provenance, warming, N addition and their interactions on plant and soil traits (Chl, SLA, LDMC, H, PD, SB, SD, MC, SOM, AP, NN, and AK). Plant origin, warming and N addition were treated as fixed factors. The within-provenance differences in leaf traits, stem traits, and soil physicochemical properties among four environments were tested using the Tukey HSD post-hoc test. All statistical analyses were performed in R 4.4.1, using base R for ANOVA and Tukey's HSD tests (Lenth 2024; R Core Team 2026).

We used Redundancy analysis (RDA) to examine the associations between plant functional traits and soil physicochemical properties under different scenarios, where leaf and stem traits served as response variables and soil physicochemical properties as explanatory variables. Mantel tests were used to quantify the correlations of plant and soil variables with climate warming, N addition, and plant source. All analyses were performed using the R package "vegan", R packages "corrplot", and the R package "ggcor" in R 4.0.2 (Huang et al. 2020; Oksanen et al. 2024; R Core Team 2020). Partial least squares structural equation models (PLS-SEMs) were used to evaluate the direct and indirect effects of warming, N addition and plant provenance on plant–soil interactions (Fig. 1c). In the RDA and PLS-SEM analyses, categorical variables were coded as binary variables: plant origin was coded as 0 for native-origin populations and 1 for invasive-origin populations, warming as 0 for ambient temperature and 1 for warming, and N addition as 0 for no N addition and 1 for N addition. Soil variables were grouped into latent variables representing soil nutrient status and soil physicochemical conditions, whereas plant traits were grouped into leaf and stem trait components. We constructed the partial least squares

method in SmartPLS 3.2.9 software to establish SEMs and utilized 5000-sample size bootstrapping to test the significance of path coefficients (Hayes 2009).

Results

Long-term warming and N addition effects on S. canadensis leaf traits

Warming alone significantly increased chlorophyll content and decreased SLA of *S. canadensis*, while N addition alone had no significant effect on leaf growth traits (Fig. 2, Table S1). Native and invasive *S. canadensis* exhibited contrasting responses in SLA and LDMC (Fig. 2b-c, Table S1). Chlorophyll content was also affected by the three-way interaction among warming, N addition, and provenance (Table S1). For *S. canadensis* from North America, warming significantly reduced SLA but exerted no significant effects on chlorophyll content and LDMC relative to the ambient; N addition had no significant influences on chlorophyll content, SLA, or LDMC; warming plus N addition significantly increased chlorophyll content and decreased SLA, while LDMC remained unchanged (Fig. 2a-c). For Chinese *S. canadensis*, warming significantly enhanced chlorophyll content and LDMC but reduced SLA relative to the ambient; N addition increased LDMC and induced no significant changes in chlorophyll content and SLA; warming plus N addition yielded leaf trait responses consistent with those of N addition (Fig. 2a-c).

Long-term warming and N addition effects on S. canadensis stem traits

Warming alone significantly increased SD but exerted no significant effects on PD, H, and SB of *S. canadensis* (Fig. 3, Table S2), whereas N addition alone had no significant effect on stem-related traits (Fig. 3, Table S2). North American *S. canadensis* had higher PD, lower SD, H and SB than Chinese *S. canadensis* (Fig. 3, Table S2). For North American *S. canadensis*, warming did not significantly alter stem-related traits relative to the ambient; N addition or warming plus N addition significantly decreased PD but induced no changes in SD, H, and SB (Fig. 3a-d). For Chinese *S. canadensis*, warming significantly increased SD while having no significant impacts on other stem-related traits relative to the ambient; N addition or warming plus N addition induced no significant changes in four stem-related traits (Fig. 3a-d).

Long-term warming and N addition effects on rhizosphere soil properties

Warming alone significantly increased soil NN but decreased AK and MC (Fig. 4b, c, e, Table S3). Nitrogen addition alone significantly altered soil AK and NN (Fig. 4b, c, Table S3). Soil AK and MC under North American *S. canadensis* were significantly lower than that those under Chinese *S. canadensis*, while NN and SOM were significantly higher for the North American *S. canadensis* (Fig. 4, Table S3). Soil AK and MC were also affected by the three-way interaction among warming, N addition, and provenance (Table S3). In addition, AK was more sensitive to provenance, warming, and N addition than other soil variables (Table S3). For rhizosphere soils associated with North American *S. canadensis*, warming or warming plus N addition significantly enhanced NN but exerted no significant effects on other variables relative to the ambient; N addition induced no significant changes in soil traits (Fig. 4a-f). For rhizosphere soil under Chinese *S. canadensis*, warming significantly increased SOM but decreased MC compared

with the ambient; N addition had no significant impacts on soil traits; warming plus N addition significantly decreased AK but increased SOM (Fig. 4b, e, f).

Relationships between plant growth traits and rhizosphere soil properties

The first two axes of the RDA explained 87.53% and 83.14% of the total variation in plant functional traits under ambient and warming, 78.17% and 90.2% under control and N addition, and 81.60% and 81.21% for North American and Chinese *S. canadensis*, respectively (Table S4). These RDA ordinations effectively quantified the associations between soil environmental factors and plant functional traits across different treatments (Fig. 5a–f, Table S4).

Available potassium contributed the most to plant trait variation under both ambient and warming, showing positive correlations with H, SB, and SD, negative correlations with PD and LDMC (Fig. 5a–b, Table S4). Compared to the ambient, warming weakened the contribution of NN but enhanced the contributions of AP and pH (Table S4). Under the ambient, NN and AP were positively correlated with SLA, chlorophyll content, and PD (Fig. 5a). Under warming environment, NN and AP remained positively correlated with PD and chlorophyll content but negatively associated with SLA (Fig. 5b). Available potassium was the dominant factor driving plant traits variation under both control and N addition, showing positive correlations with H, SD, SB, and SLA, but negative correlations with LDMC and PD (Fig. 5c–d, Table S4). Compared to the control, N addition increased the contributions of NN and AP but decreased the contributions of SOM and pH (Table S4). Specifically, AP was positively associated with SLA and PD under the control; but remained positively correlated with PD while negatively correlated with SLA under N addition (Fig. 5c–d). Soil NN, SOM, and AP were the dominant factors explaining traits variation in North American *S. canadensis*, while soil pH, AK, and NN primarily explained the traits variation of Chinese *S. canadensis* (Table S4). For North American *S. canadensis*, soil NN was positively correlated with chlorophyll content, LDMC, and SD but negatively correlated with SLA (Fig. 5e). By contrast, NN was positively correlated with H, SD, and SLA but negatively correlated with chlorophyll content and LDMC in Chinese *S. canadensis* (Fig. 5f).

Provenance significantly correlated with all plant and soil traits except PD, chlorophyll content, pH, NN and AP; warming significantly correlated with pH, SOM, AP, AK, NN, SLA, and chlorophyll content; N addition significantly correlated with AP, NN, and AK but showed no significant relationships with other traits (Fig. 6). In terms of plant growth, stem biomass showed significant negative correlations with MC, SOM, PD, and LDMC, and positive correlations with AK, SD, H, and LA; LDMC was significantly positively correlated with AP, and significantly negatively correlated with AK, SD, H, LA, and SLA (Fig. 6).

Warming had significant positive direct effects on leaf traits and stem traits ($\beta = 0.440$ and $\beta = 0.357$, respectively) (Fig. 7a). Warming also had significant indirect effects on stem traits by negatively altering soil physicochemical properties ($\beta = -0.048$), while its indirect effect on leaf traits was non-significant (Fig. 7a). Plant provenance exhibited significant positive effects on leaf and stem traits ($\beta = 0.926$ and $\beta = 0.712$, respectively, Fig. 7b), and significant negative effects on soil physicochemical properties ($\beta = -0.582$), but had no significant effects on soil nutrient properties (Fig. 7b). Soil nutrient and

physicochemical properties had no significant effects on leaf or stem traits (Fig. 7b). Nitrogen addition exhibited no significant effects on leaf traits, stem traits, soil physicochemical properties, and soil nutrient properties (Fig. 7c).

Discussion

Based on the long-term warming and N addition experiment, we systematically examined how climate warming, N deposition and plant provenance affect leaf and stem traits of *S. canadensis* and their relationships with soil properties. We found that: (1) warming and plant provenance had strong effects on leaf and stem traits than N addition, with chlorophyll content being significantly affected by the three-way interaction among warming, N addition and provenance; and (2) leaf and stem traits were significantly regulated by soil nutrients; warming, N addition, and plant provenance altered the relationships between plant traits and soil properties. Overall, our results highlight the phenotypic plasticity and adaptive mechanisms of an invasive plant under climate warming and nutrient change, and emphasize the key role of provenance in mediating resource-use strategies and invasion potential under climate changes.

Independently effects of warming and plant provenance on leaf and stem traits

Warming significantly increased chlorophyll content and SD of *S. canadensis* (Fig. 2; Fig. 3), consistent with previous evidence showing warming and N addition can increase leaf chlorophyll to improve photosynthesis (Ren et al. 2022a). This is likely attributed to warming-stimulated carbon assimilation and altered resource allocation, which diverts more carbon to stem growth and expands stem thickness (Yang et al. 2023). However, warming reduced SLA (Fig. 2), producing to thicker and denser leaves that lower transpiration and strengthen heat resistance (Bao et al. 2022). From a leaf economics spectrum perspective, lower SLA represents a typical resource-conservative adaptation strategy, as greater biomass investment per unit leaf facilitates plants adaptation to heat and drought (Wright et al. 2004). During this process, higher chlorophyll content may offset the diminished leaf area to sustain stable area-based photosynthesis (Yang et al. 2023). Taken together, these coordinated trait suggests a shift from fast to slow investment-return strategies under warming, which may further improve the competitiveness and invasion capacity of *S. canadensis* under warmer climates (Sastry and Barua 2017).

Our results also revealed that the invasive provenance exhibited higher SLA and lower LDMC than native provenance, indicative of a more acquisitive carbon-use strategy (Fig. 2). Furthermore, provenance also modulated the responses of leaf functional traits to warming and N addition. For instance, warming, N addition, and warming plus N addition significantly increased LDMC of invasive provenance compared to the control, whereas LDMC of native provenance showed no significant changes (Fig. 2). This divergent response demonstrates stronger phenotypic plasticity in invasive provenances (Brandenburger et al. 2020; Valliere et al. 2019). However, Peng et al. (2019) reported no significant effects of warming and N addition on LDMC of *S. canadensis*, which is inconsistent with our results. This divergence may stem from their distinct invasion histories: native provenance has a shorter invasion history, whereas invasive

populations have evolved adaptive trait modifications over longer invasion history. After ten years of treatments, invasive provenance plants exhibited greater trait plasticity and superior stress tolerance (Hasigerili et al. 2023; Zhou et al. 2022). This finding highlights the adaptive advantage of invasive plant provenances under climate change and aligns with the conclusion that invasive plants generally exhibit higher phenotypic plasticity (Brandenburger et al. 2020; Volis et al. 2015). For stem functional traits of *S. canadensis*, native provenance had shorter plant height, smaller stem diameter, and lower stem biomass, higher plant density relative to native provenance (Fig. 3). This result matches prior research on divergent growth strategies between invasive and native *S. canadensis* populations (Qiang et al. 2021). A plausible mechanism is that reduced pressure from natural enemies and pathogens in introduced ranges enables *S. canadensis* to reallocate resources from defense toward growth and competitive performance (Blossey and Nötzold 1995; Keane and Crawley 2002). Such resource reallocation promotes a low-density–high individual performance strategy: fewer individuals occupy per unit area, yet each plant develops greater competitive capacity and expansion potential under resource-limitations (Poljuha et al. 2024). This strategy explains why invasive provenance plants grow taller with thicker, more robust stems. According to the classice size–density trade-off, larger individual biomass inevitably reduces the maximum number of plants a fixed area can sustain, thereby lowering stand density (Westoby 1984).

In addition, N addition alone had no significant effects on leaf and stem functional traits, only chlorophyll content responded significantly to the three-way interaction of three factors (Fig. 2; Fig. 3). Nitrogen is essential for chlorophyll synthesis and photosynthesis (Correa et al. 2022; Lv et al. 2025), while warming reshapes plant N demand and soil N turnover rates, potentially modifying the magnitude of N addition effects on chlorophyll (Sharwood et al. 2017; Tingey et al. 2003). Distinct inter-provenance divergence in phenotypic plasticity and resource allocation strategies further drives the pronounced three-way interactive regulation of chlorophyll (Brandenburger et al. 2020; Ren et al. 2022a). This pattern is consistent with previous finding that warming and N addition can jointly influence the performance of *S. canadensis*, and that such responses may be modulated by plant sources (Ren et al. 2022a; Zhou et al. 2025). The non-significant main effect of nitrogen arises from the broad-spectrum N acquisition of *S. canadensis*. Variable N uptake and resource partitioning alter trait responses to exogenous N; mismatched N forms or accessible alternative soil N pools eliminate consistent N effects, which only vary under provenance–warming combinations (Yu et al. 2016; Zou et al. 2022). Overall, temperature acts as the dominant environmental driver, whereas nitrogen effects emerge through joint interactions with warming and soil nutrient processes (Sharwood et al. 2017; Tingey et al. 2003).

Differential responses of plant leaf and stem traits to edaphic properties under warming, N addition, and provenance

Warming significantly increased soil NN but decreased soil AK and MC (Fig. 3). Such shifts may be attributed to warming-induced acceleration of organic matter decomposition, N mineralization and nitrification, thereby boosting NN availability (Sun et al. 2024; Tingey et al. 2003; Yang et al. 2022). Meanwhile, warming may enhance evapotranspiration and deplete soil moisture (Kinugasa et al. 2024). For instance, reduced soil moisture content diminishes the diffusion and convective replenishment of

AK, while intensifying plant interspecific competition for its acquisition, jointly decreasing soil AK (Bai et al. 2013; Kinugasa et al. 2024). Soil AK and NN were also significantly altered by N addition (Fig. 4). Exogenous N inputs can directly raise soil nitrate N, but long-term N enrichment acidifies soils and promotes leaching of base cations, which depletes soil AK (Li and Li 2025; Shan et al. 2018). Rhizosphere soils associated with native provenances exhibited significantly lower AK and MC, but higher NN and SOM relative to soils under invasive provenances (Fig. 4; Table 4). This provenance-driven edaphic variation demonstrates that intraspecific provenance may regulates the variation in plant–soil interactions and nutrient-cycling processes. Ye et al. (2019) indicated that *S. canadensis* can increase soil AK through root exudates and the recruitment of K-solubilizing microorganisms. In turn, increased soil AK may promote the growth and invasive capacity of invasive provenance populations, which is consistent with our results (Vipanchika et al. 2024). Provenance divergence remodels plant functional traits and resource-use strategies, thereby modifying soil processes through litter quality, root exudation and interactions with soil microbial communities (Zhou et al. 2025).

We also found a significant three-way interaction of warming, N addition, and provenance on AK. This interactive pattern can be explained by coupled nitrogen transformation and cation leaching processes: ammonium nitrification releases hydrogen ions, which displace exchangeable K^+ into the soil solution, and subsequent nitrate leaching drives the loss of potassium (Baer et al. 2023; Hamidi et al. 2021). Meanwhile, warming accelerates organic matter mineralization and reinforces K leaching (Sun et al. 2024; Yang et al. 2022). Combined warming and N addition inhibited the conversion of insoluble K into plant available forms (Oduor et al. 2022), reducing AK and slowing nutrient turnover to produces this three-way interactive effect (Oduor et al. 2022; Yuan et al. 2013).

Multiple lines of statistical evidence consistently AK act as the predominant edaphic factor regulating leaf and stem functional traits of *S. canadensis*. The RDA prioritized AK as the strongest explanatory variable for plant trait variation across warming and N addition; similarly, correlation heatmap revealed a significant negative relationship with LDMC (Fig. 5–6). In the PLS-SEM under the N-addition scenario, the soil nutrient traits mainly represented by AK, NN and AP, also exerted a positive effect on leaf traits. These coordinated responses reflect a key plant–soil feedback strategy of invasive *S. canadensis*, which can alter soil AK via root exudation and recruitment of potassium-solubilizing microorganisms, and AK may influence plant stem and leaf growth by regulating osmotic balance, stomatal function, assimilate transport and cell expansion (Sardans and Peñuelas 2021; Ye et al. 2019). When available K is not sufficient, *S. canadensis* may shift toward a resource-conservative strategy characterized by modified vegetative growth and low leaf construction cost (Vipanchika et al. 2024), thereby explaining the higher stem diameter and smaller leaves under warming. Together, these results suggest that AK may act as a key soil nutrient factor linking soil resource availability with the growth and functional trait responses of *S. canadensis* global change.

In addition, heatmap and RDA showed negative correlated of SOM with stem traits (Fig. 5–6), PLS-SEM further confirmed significant negative pathways linking soil physicochemical properties to stem/leaf traits under warming and N addition (Fig. 7). Such suppression is primarily attributed to high SOM-

induced soil waterlogging and rhizosphere hypoxia, which restrict root activity and stem growth (Liu et al. 2026; Ma et al. 2018; Zhu et al. 2026). Excessive organic inputs may also promote microbial N immobilization, temporarily reducing plant-available N and a conservative leaf strategy with higher LDMC and lower SLA (Cao et al. 2021). Additionally, soil pH soil pH exhibited context-dependent trait regulation across provenances and treatments, as pH-mediated nutrient availability varies with environmental limiting resources (Barrow and Hartemink 2023).

Environment changes substantially modified the resource-use strategies of *S. canadensis*. Warming weakened the positive effect of nitrate N on SLA and shifted *S. canadensis* toward a conservative, slow investment–return strategy. This interpretation is broadly consistent with previous findings showing that plant strategies can shift toward more conservative trait syndromes under stressful environmental conditions (Dostálek et al. 2020).Although N addition direct effects on stem and leaf traits were weak and unstable, confirming N addition had limited influence on plant traits (Wan et al. 2018); its alter soil AK and NN, and reshaped relationships among plant and soil variables. Importantly, plant provenance had strong positive paths to leaf and stem traits and modulated plant–soil interactions. This indicates that native and invasive populations of *S. canadensis* employ distinct adaptive strategies under changing environments, highlighting the critical role of intraspecific variation in mediating plant trait plasticity of *S. canadensis* (Zhou et al. 2025).

Conclusions

This study clarifies the mechanisms underlying plant invasion under global change by integrating aboveground leaf and stem traits and rhizosphere edaphic properties of *S. canadensis*. Warming alone significantly increased chlorophyll content and stem diameter but decreased SLA; N addition alone showed no significant effects on these traits; invasive provenance had higher SLA, plant height, stem diameter and biomass, but lower LDMC and plant density than native provenance. For rhizosphere soils, warming significantly elevated soil nitrate N but decreased available potassium and moisture; N addition significantly altered soil available potassium and nitrate N. Invasive-associated soils contained more available potassium and moisture, but less nitrate N and soil organic matter than native-associated soils. Warming, N addition, and provenance regulate the relationships among leaf traits, stem traits, and edaphic properties. Specifically, soil available potassium was the dominant driver of plant traits variation under both warming and N addition, positively correlating with plant height, stem diameter and biomass, but negatively correlating with LDMC. The relationship between LDMC and nitrate nitrogen exhibited opposite trends in native versus invasive provenances.

However, we failed to examine root phenotypes, including fine-root morphological plasticity, root exudates and rhizosphere microbial communities. Numerous studies have confirmed that climate change modulates root morphology and root–microbe and leaf–root trait coordination (Ma et al. 2018; Liu et al. 2026; Zhu et al. 2026). For instance, thick-rooted plants rely more on mycorrhizal symbiosis and adopt a conservative underground resource-acquisition strategy (Ma et al. 2018). To comprehensively decipher climate change impacts, future work should explore the root economics spectrum and trait

coordination among leaves, stems and fine roots. Overall, our results reveal the adaptive strategies of *S. canadensis*, offering theoretical support for forecasting its invasion risk and distribution under future global change.

Abbreviations

AK
Available potassium
AP
Available phosphorus
Chl
Chlorophyll content
H
Plant height
LDMC
Leaf dry matter content
MC
Moisture content
NN
Nitrate nitrogen
PD
Plant density
PLS-SEM
Partial least squares structural equation modelling
RDA
Redundancy analysis
SB
Stem biomass
SD
Stem diameter
SLA
Specific leaf area
SOM
Soil organic matter

Declarations

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data are available on request from the authors.

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Figures

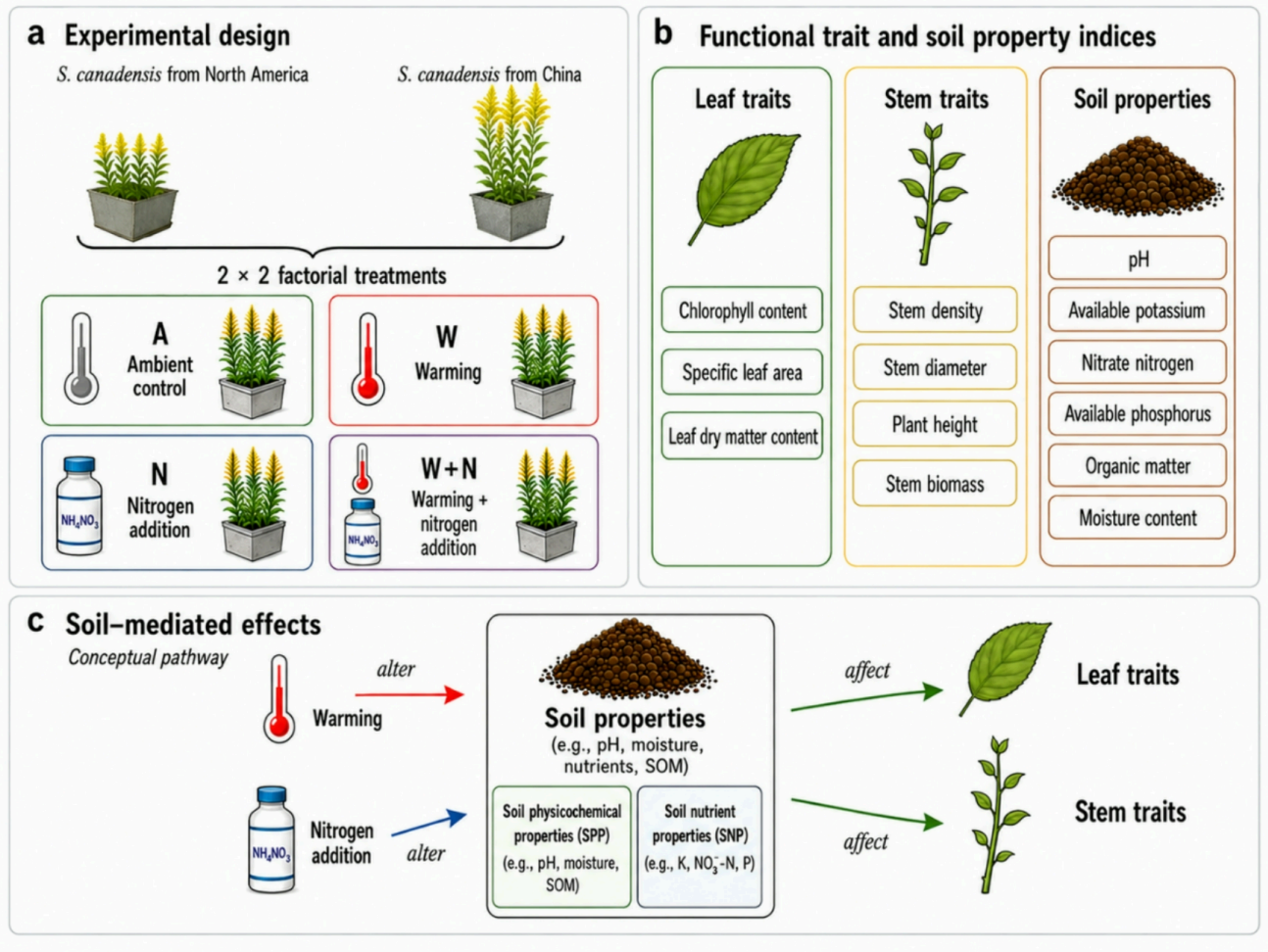


Figure 1

This figure illustrates the experimental design, measurement indicators, and soil-mediated effects. Fig.1a shows the experimental design involving three factors, which are maternal provenance (*S. canadensis*from North America [NA] or from China [CN]), climate scenario (ambient [A] or warming [W]), and Nitrogen addition (ambient [A] or N addition [N]). Fig.1b shows the measured traits into three groups of plant and soil. Leaf growth related indicators include chlorophyll content (Chl), specific leaf area (SLA), and leaf dry matter content (LDMC); stem growth related indicators include plant stem density (PD), stem diameter (SD), plant height (H), and stem biomass (SB); soil physicochemical indicators include pH, available potassium (AK), inorganic nitrogen (NN), available phosphorus (AP), soil organic matter (SOM), and moisture content (MC). Fig.1c shows how warming and nitrogen addition alters soil properties to mediate leaf and stem functional traits.

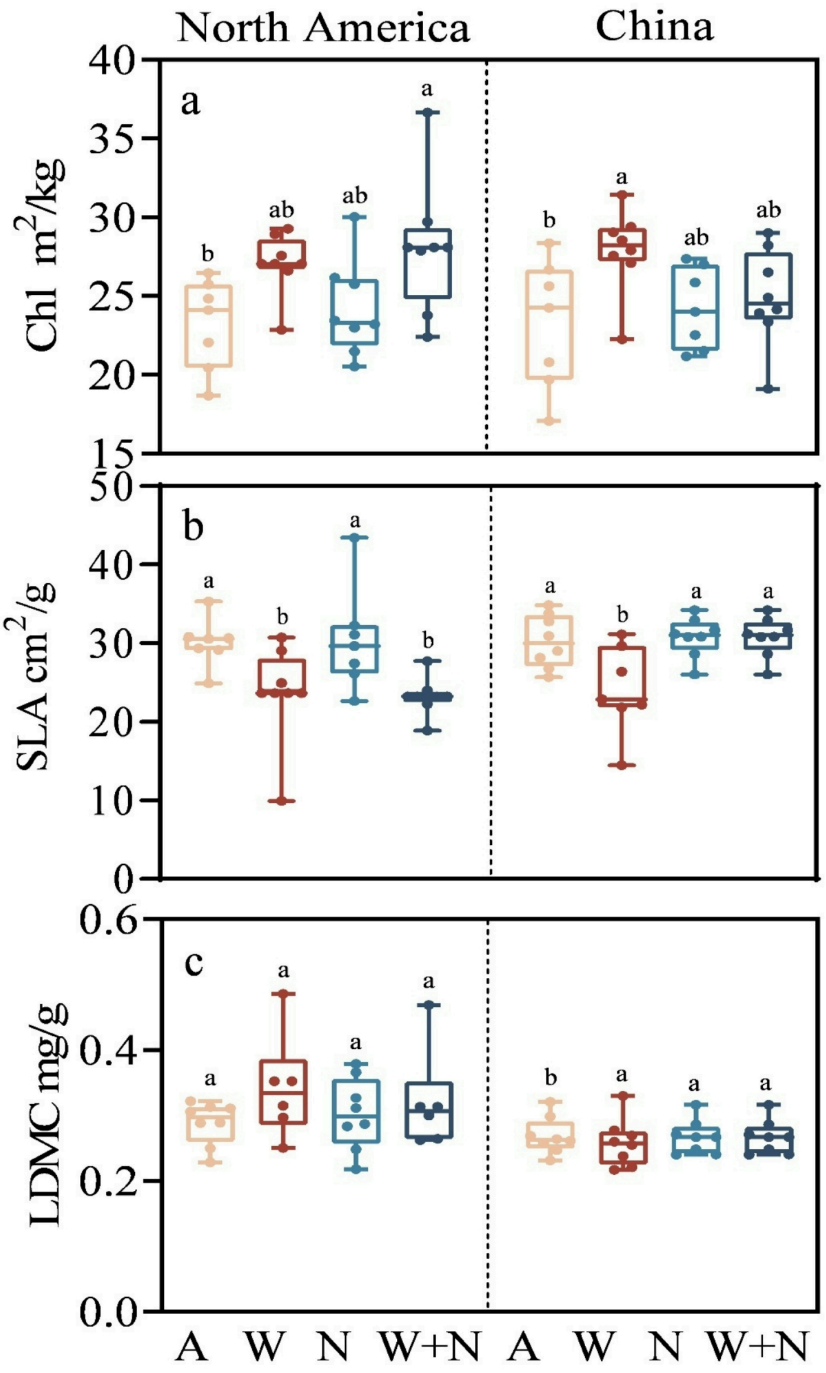


Figure 2

Effects of warming and N addition on leaf traits of *S. canadensis*. This figure shows treatment effects on leaf functional traits of *S. canadensis* from North America and China. Panels display (a) chlorophyll content (Chl), (b) specific leaf area (SLA), and (c) leaf dry matter content (LDMC) under four treatments: ambient (A), warming (W), N addition (N), and warming plus nitrogen (W+N).The lines in the box represent the mean values, box boundaries indicate the values in the 25th–75th percentile range, and

whiskers indicate the min to the max. Different letters indicate significant differences among combinations at *P*<0.05. Detailed statistical analyses are given in Table 2.

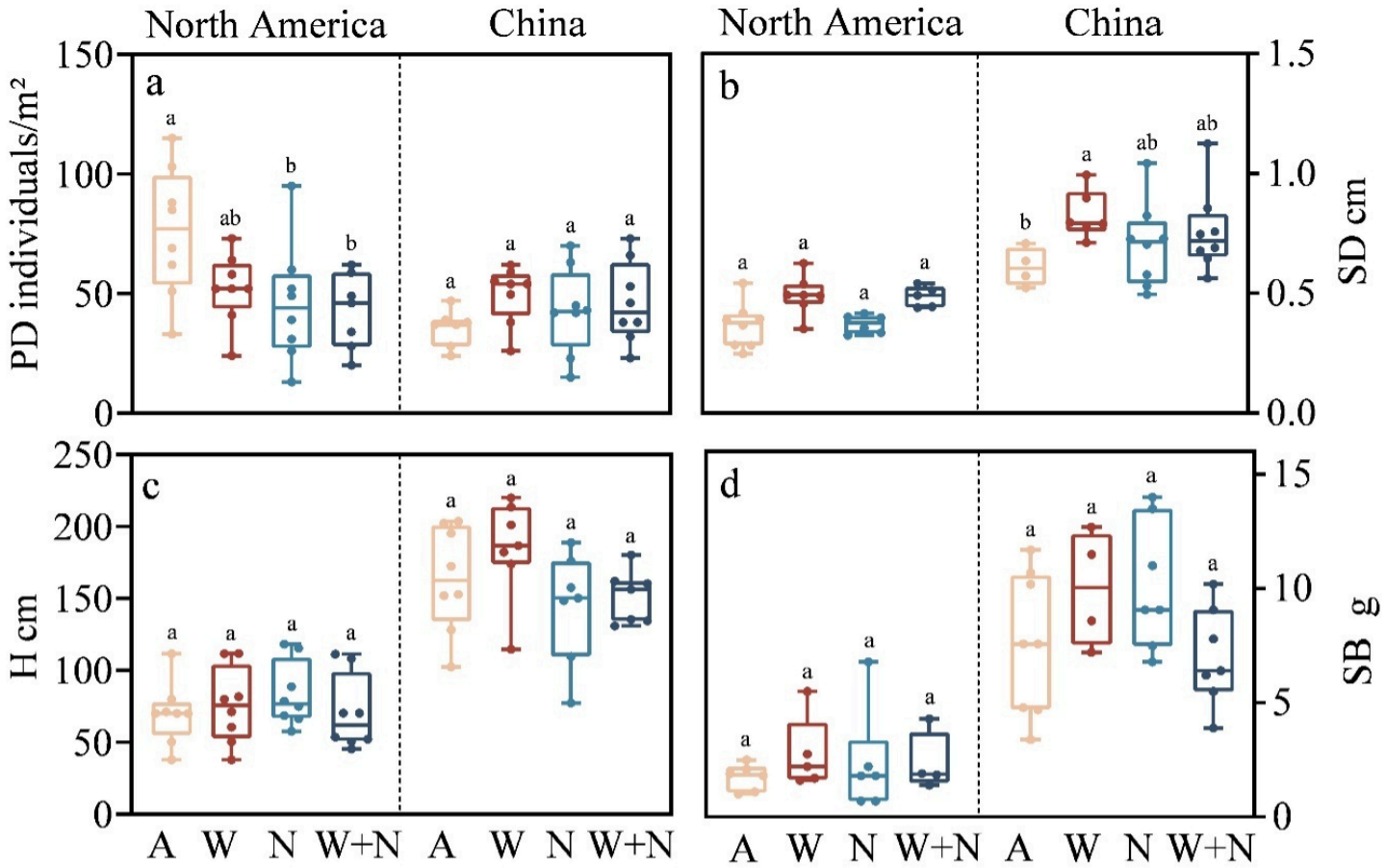


Figure 3

Effects of warming and N addition on *S. canadensis* stem traits. Panels show (a) plant density (PD; individuals m^{-2}), (b) stem diameter (SD; cm), (c) plant height (H; cm), and (d) stem biomass (SB; g) under four treatments: ambient (A), warming (W), N addition (N), and warming plus nitrogen (W+N).The lines in the box represent the mean values, box boundaries indicate the values in the 25th–75th percentile range, and whiskers indicate the min to the max. Different letters indicate significant differences among combinations at P<0.05. Detailed statistical analyses are given in Table 3.

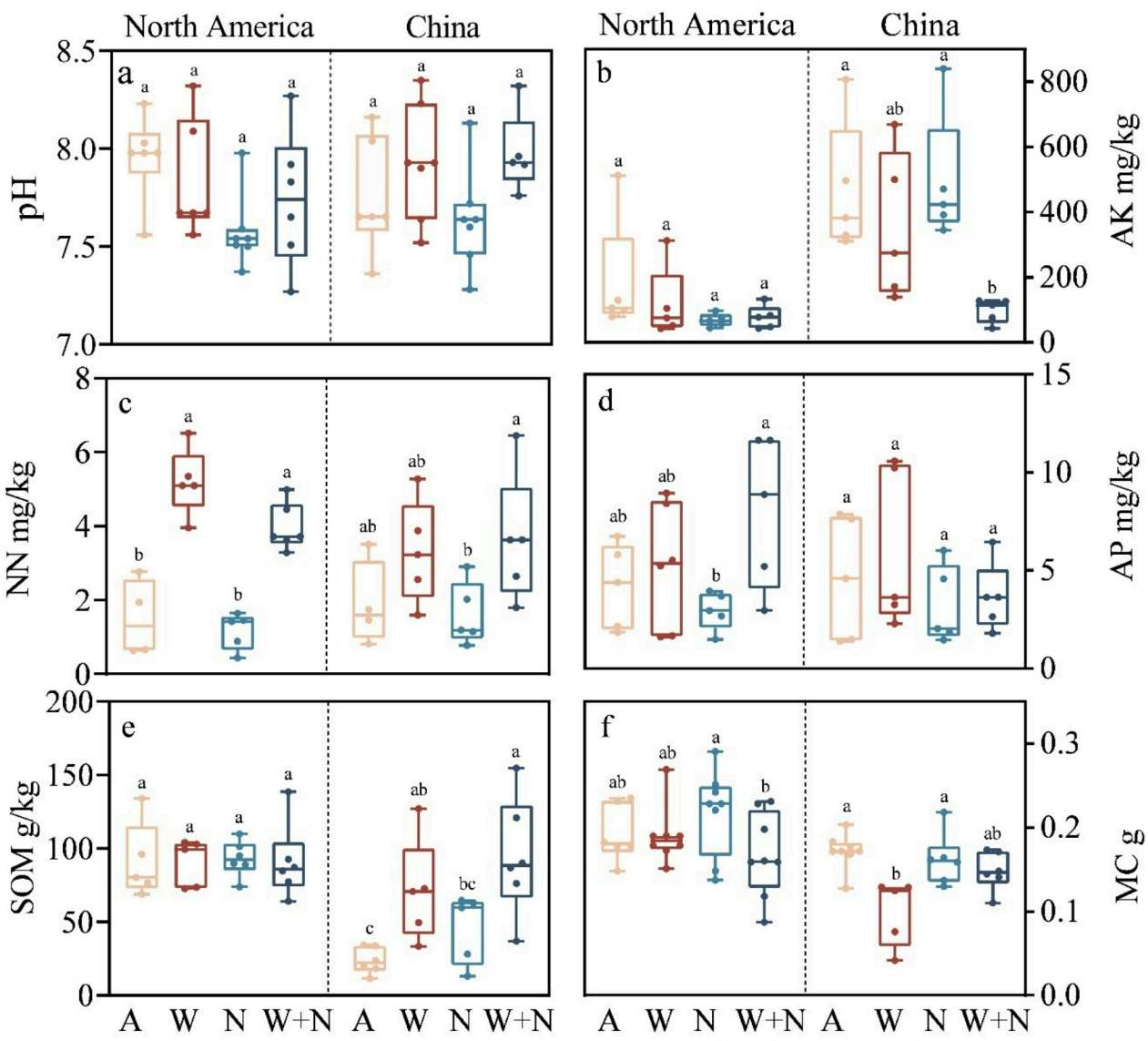


Figure 4

Effects of warming, N addition, and provenance on rhizosphere soil properties of *S. canadensis*. Panels present (a) soil pH, (b) available K (AK; mg kg^{-1}), (c) nitrate N (NN; mg kg^{-1}), (d) available P (AP; mg kg^{-1}), (e) soil organic matter (SOM; g kg^{-1}), and (f) soil moisture content (MC; g g^{-1}). The lines in the box represent the mean values, box boundaries indicate the values in the 25th–75th percentile range, and whiskers indicate the min to the max. Different letters indicate a significant difference among combinations at $P<0.05$. Ambient, A; warming, W; nitrogen addition, N; warming plus nitrogen, W+N. Detailed statistical analyses are given in Table 4

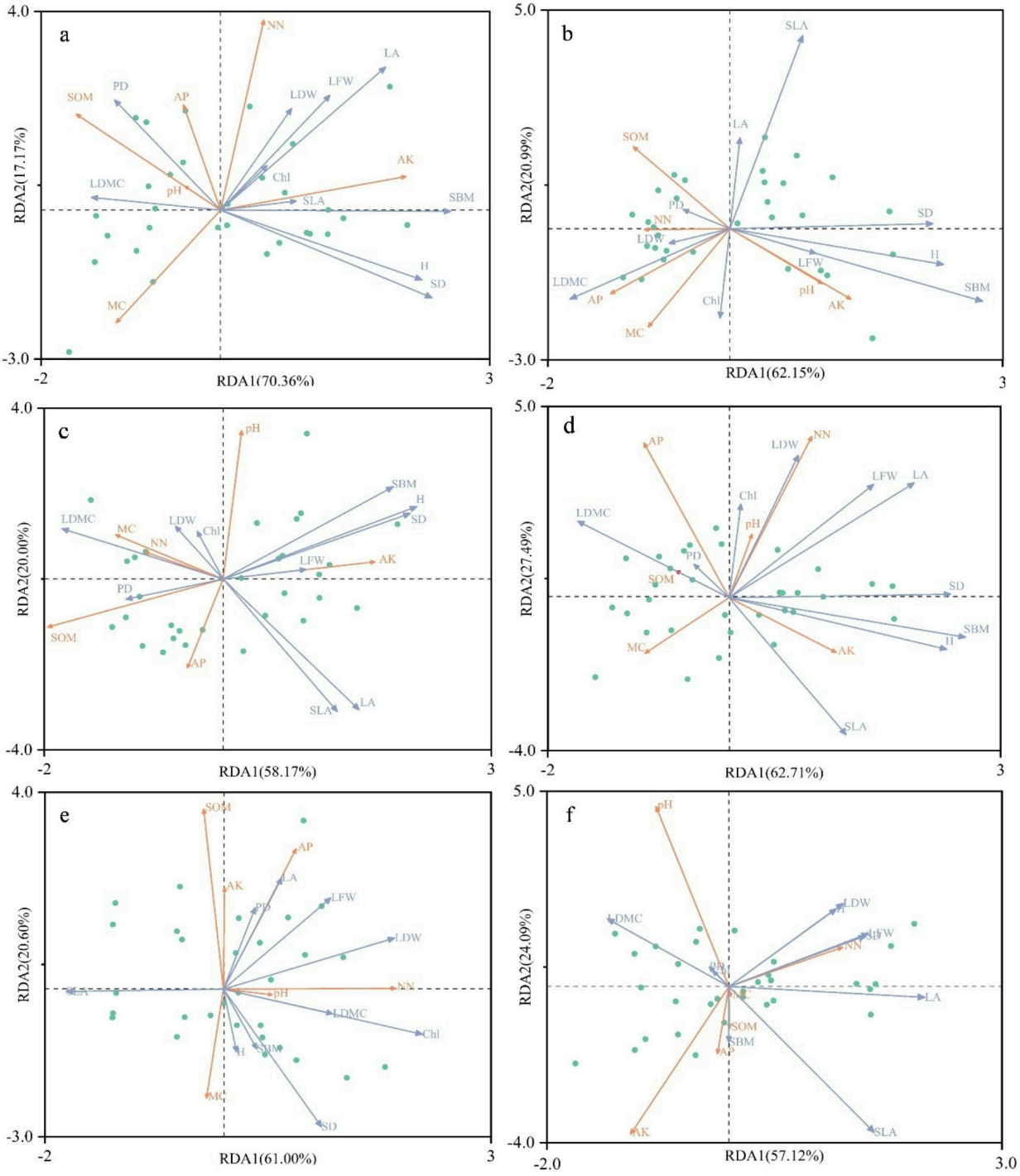


Figure 5

Redundancy analysis (RDA) illustrating the relationships between plant traits (blue vectors) and soil environmental variables (orange vectors) under different environments. Panels (a) and (b) represent ambient and warming, respectively; panels (c) and (d) represent control and N addition, respectively; panels (e) and (f) represent North American and Chinese provenances, respectively. Points denote

individual samples. The direction and length of vectors indicate the direction and strength of correlations with the ordination axes, while the angles between vectors reflect correlations among variables.

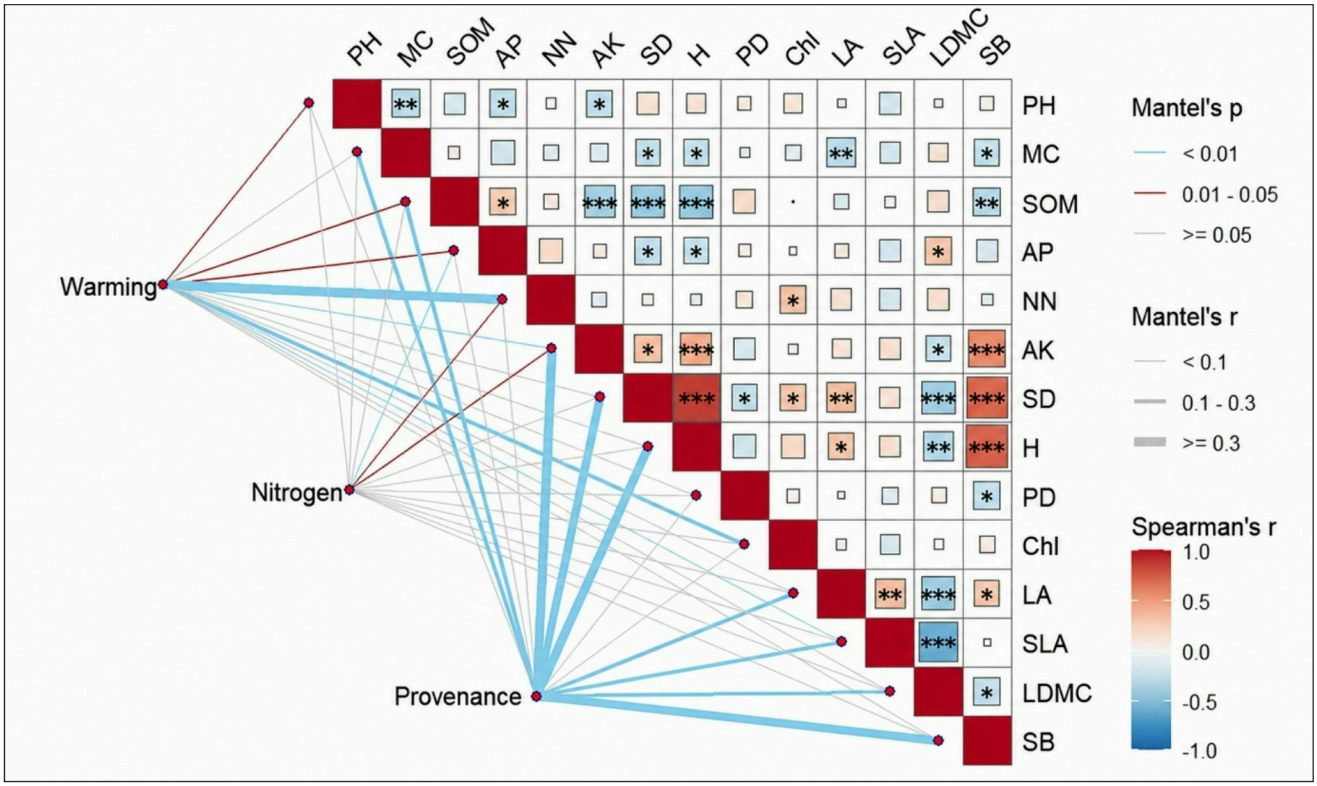


Figure 6

Combined correlation–Mantel analysis linking experimental factors, soil properties, and plant traits. The upper triangular heatmap shows pairwise Spearman's rank correlations among variables (color scale from negative to positive), with asterisks indicating significance levels ($P < 0.05$, $P < 0.01$, $P < 0.001$). The network summarizes Mantel test results for the effects of warming, N addition, and source (provenance) on the multivariate trait–soil matrix: line color denotes Mantel's P value (< 0.01, 0.01–0.05, ≥ 0.05) and line width indicates Mantel's r (effect size). Variables include soil pH (pH), soil moisture content (MC), soil organic matter (SOM), available phosphorus (AP), inorganic nitrogen (NN), available potassium (AK), and plant traits (SD, H, PD, Chl, LA, SLA, LDMC, SB).

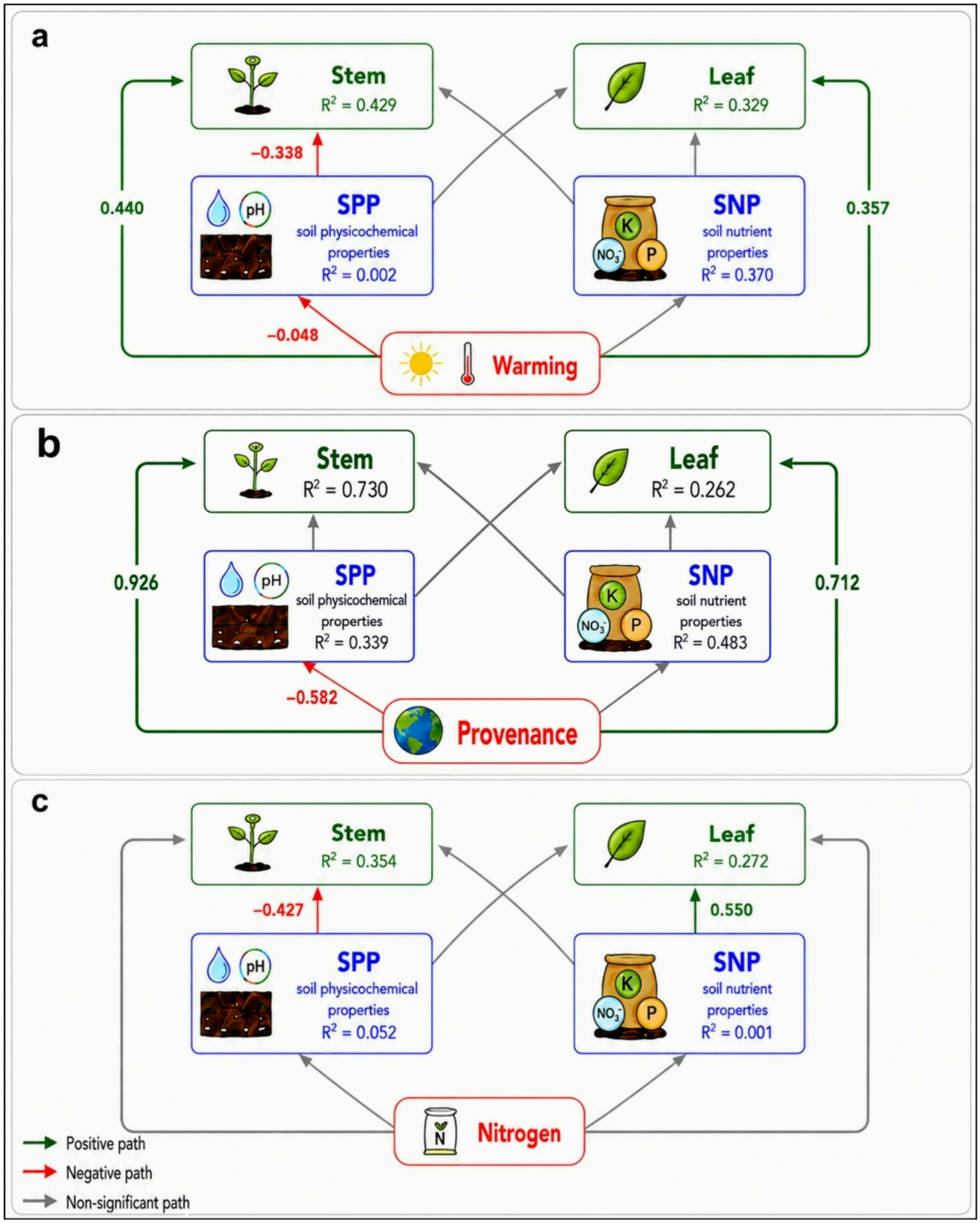


Figure 7

Structural equation models (SEMs) illustrating the direct and indirect effects of (a) warming, (b) nitrogen addition (nitrogen), and (c) source (provenance) on plant leaf and stem trait modules mediated by soil properties. Stem and leaf represent stem-related and leaf-related traits, SPP and SNP denote soil physicochemical properties and soil nutrient properties. The color of the lines indicates the relationship

between variables (green/positive, red/negative), while gray arrows denote non-significant paths. The values within the boxes represent R^2, indicating the coefficient of determination.

Supplementary Files

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- SupplementaryMaterial.docx