

Research Article

Winter leaf phenology differences facilitate selective control of an invasive plant species by herbicide

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Abstract

Herbicide control of invasive plant species is generally efficient. However, there is a likelihood of the excessive application of non-selective herbicides that kill co-occurring native species and cause environmental toxicity. We present a case study on the control of the invasive exotic *Solidago canadensis* with photosynthetically active leaves in winter by applying glyphosate. This approach improves herbicide control efficiency, while preventing harm to most co-occurring native plants. We quantified the winter leaf phenology and photosynthetic capacity of *S. canadensis* and two commonly co-occurring native species. We tested the effects of glyphosate and competition on *S. canadensis* and native *Imperata cylindrica* with contrasting winter leaf phenology in both pot and field experiments. Finally, we surveyed the life forms and winter leaf phenology of most co-occurring plant species in eastern China to determine whether most co-occurring species and *S. canadensis* differ in winter leaf phenology. Old leaves withered much later and new leaves developed much earlier in *S. canadensis* than in the two co-occurring species. Both the old and new leaves of *S. canadensis* had high photosynthetic capacity in winter. In summer, glyphosate suppressed the growth of *S. canadensis* by 20.1–59.5% and growth of *I. cylindrica* to a greater extent (by 57.6–91.7%), whereas winter application of glyphosate at a certain concentration suppressed the growth of *S. canadensis* by 91.4–95.6% (the efficiency was higher than summer application), but had no impact on *I. cylindrica*. Glyphosate application in winter alleviated competition stress from *S. canadensis* on *I. cylindrica*. We conclude that winter glyphosate application can increase the selectivity and efficiency of chemical control of invasive *S. canadensis*, which may shift the competition balance towards native species and favour native vegetation recovery in sites invaded by *S. canadensis*. The principles of this approach can be applied to any scenario where invasive species and co-occurring species have distinct phenological niche separation.

Key words: Clonal plants, competition, glyphosate, photosynthesis capacity, rhizome, *Solidago canadensis*



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Introduction

Biological invasions are amongst the greatest threats to indigenous biodiversity, ecosystem services and economic development globally (van Kleunen et al. 2015; Early et al. 2016; Head 2017; Adomako et al. 2019; Roiloa et al. 2020). Invasive exotic plant species are typically larger, accumulate more biomass, form

considerable monocultural patches and, eventually, exclude native plants from invaded sites (van Kleunen et al. 2010; Drenovsky et al. 2012; Godoy et al. 2012; Wang et al. 2017, 2019). Dramatic changes in local vegetation structure caused by the invasion of exotic plant species can lead to fundamental changes in ecosystem functions, which are usually degraded by biodiversity loss (Hejda et al. 2009; Vilà et al. 2011; Peller and Altermatt 2024).

Management of invasive species — by inhibiting growth, population increase and expansion — is necessary for biodiversity conservation (Mačić et al. 2018; Gentili et al. 2021; Sherrill et al. 2022). However, tackling exotic invasive species is challenging because they usually have a high growth capacity and resistance to stresses and disturbances (van Kleunen et al. 2010; Drenovsky et al. 2012; Godoy et al. 2012). Common practices for controlling invasive species include physical removal by pulling out or mowing and chemical control by spraying herbicides (Sebastian et al. 2017; Mahmood et al. 2018), biological control by introducing natural enemies (Pratt et al. 2013) and restoration of native species to increase ecological resistance (Byun et al. 2018). These approaches vary in their cost and effectiveness for the eradication of exotic invasive plants, depending on the species in question and the stage of socioeconomic development in the area (Weidlich et al. 2020).

Phenology is an essential functional trait that can be used to distinguish invasive species from native species, based on their different temporal niches throughout the season (Fridley 2012; Wolkovich and Cleland 2014; Park et al. 2024). Several studies have reported that exotic species have extended growth season length, due to an earlier start of growth period and/or later senescence (Polgar et al. 2013; Smith 2013; Wilsey et al. 2018). These differences have been considered an important factor driving invasion success (Fridley 2012; Rejmánek 2013) by filling vacant temporal niches, enhancing resource pre-emption or growth (priority effects or prolonged growth period) (Wolkovich and Cleland 2011) or, possibly, via alteration of allelopathy, apparent competition or pollination (Smith 2013; Smith and Hall 2016). The impact of phenological differences on exotic species invasion can be more pronounced with global changes such as increased nitrogen deposition (Valliere et al. 2022). Furthermore, competition may also alter phenology, for example, a reduction in lifespan (Levine et al. 2024). Thus, phenological niche differences may offer resource managers the opportunity to control exotic species, while protecting native species (Wolkovich and Cleland 2011; Hess et al. 2019; Taylor et al. 2020).

Amongst these different approaches, the application of herbicides is common and usually effective (Wagner et al. 2017; Mahmood et al. 2018). However, most herbicides do not have high specificity, resulting in a “non-target effect”, in which native plant species may be damaged as much as or greater than the target species (Gibson et al. 2019; Peterson et al. 2020). Furthermore, excessive herbicide use may increase the risk of environmental toxicity (Richmond 2018; Peterson et al. 2020; Gandhi et al. 2021) and promote the development of herbicide-resistant populations of exotic species (Baucom 2019). Gu et al. (2017) reported that application of glyphosate at high doses in the growing season could depress growth and caused mortality of a common co-occurring plant species to a greater extent than that of invasive *Solidago canadensis*. Consequently, when applying chemical controls, both the dosage of herbicides and their potential harm to native species must be reduced as much as possible.

Progress has been made in the use of phenological differences to control invasive plant species. Wainwright et al. (2012) showed that manipulation of earlier rainfall stimulated early germination of exotic species in unfavourable seasons, but not of native species, which led to high mortality of exotic species and may favour native species restoration. Planting early native species early in the season or fast-growing species after the removal of invasive species can effectively suppress the growth of exotic species (Smith et al. 2021; Kumar et al. 2024). It has been suggested that phenological differences can be utilised to increase the selectivity of herbicides in controlling invasive species during seasons when invasive species are active and native species are inactive (Wolkovich and Cleland 2011). Caplan et al. (2018) showed that herbicide application can still be effective in late autumn for control of invasive *Lonicera* species with delayed leaf senescence. It remains unclear how herbicide control of invaders may affect neighbouring native species and their interactions with invaders.

Solidago canadensis (Asteraceae), commonly known as Goldenrod, is native to North America, but has become invasive in Asia, Europe and Australia (Perera et al. 2021; Qiang et al. 2021). Due to its highly competitive capacity, *S. canadensis* replaces native plant species, forming large patches of monocultures and causing a decrease in the diversity of native plant species (Szymura and Szymura 2016; Adomako et al. 2022; Ye et al. 2022; Xie et al. 2023). To date, no efficient or environment-friendly methods have been developed to control this species. In eastern China, invasive *S. canadensis* has a winter phenology that differs from that of the co-occurring species. Mature leaves of *S. canadensis* senesce much later in the season than the leaves of most co-occurring plant species and new ramets and leaves appear in early autumn — far earlier than in most native species, which do not start growing until early spring. A preliminary test also showed that both old but viable leaves and newly-grown leaves of *S. canadensis* are photosynthetically active in winter, whereas the completely senescent leaves of most native co-occurring plant species are inactive. As most herbicides are only effective after being absorbed by green leaves or viable roots (Sterling 1994; Nandula and Vencill 2015), it is possible that herbicides may only injure *S. canadensis*, leaving native plant species — with dormant aboveground parts — unaffected. Although it is recognised in practice that some herbicides, such as glyphosate, can still be effective in winter as long as the air temperature is above a certain threshold value, there are very few studies on the effects of herbicide application on target plants in winter. Badalamenti et al. (2015) reported significant seasonal effects of herbicides on the mortality rate and re-sprouting ability of invasive *Ailanthus altissima* under Mediterranean climatic conditions, indicating the possibility of improving control efficiency by selecting optimal seasons. Furthermore, studies on the effects of herbicides on growth and competition between invasive plants and co-occurring native plants with contrasting winter phenologies have not yet been reported.

In the present study, we tested the feasibility of applying glyphosate, a commonly used herbicide (Duke and Powles 2008; Richmond 2018; Gandhi et al. 2021), to control *S. canadensis*, while avoiding harming co-occurring species in winter. First, we quantified the differences in winter leaf phenology and photosynthetic capacity between invasive *S. canadensis* and two co-occurring species. Second, in both field and pot experiments, we compared the responses of *S. canadensis* and a common native co-occurring species with contrasting winter leaf phenology to

glyphosate application during summer and winter. We hypothesised that winter glyphosate application would inhibit the growth of *S. canadensis* with photosynthetically active leaves, but not that of the native species with dead leaves. Finally, we surveyed the life forms and related winter leaf phenology of most co-occurring species of *S. canadensis* in eastern China to clarify whether this strategy can be applied to *S. canadensis* at various sites.

Materials and methods

Study sites

The pot and field experiments described below were conducted in Fuyang, Hangzhou, Zhejiang Province, China (29.7–30.2°N, 119.4–120.1°E), where the invasive plant *S. canadensis* is widely distributed. This area is characterised by a typical subtropical monsoon climate with four distinct seasons. The terms summer and winter in this study are defined according to the Chinese National Standards (GB/T 42074-2022) (Standardization Administration of China 2022). Specifically, summer and winter start when daily mean temperature of five consecutive days is above 22 °C and below 10 °C, respectively. Summer (May – September) is hot and wet and winter (December – February) is relatively cold and dry. During winter, the mean daily maximum air temperature is 11 °C in December, 8 °C in January and 11 °C in February (Suppl. material 1). The mean daily minimum air temperatures in these three months are 3, 1 and 3 °C, respectively and the mean monthly precipitation is 51, 72 and 85 mm, respectively (Suppl. material 1). The mean daily air temperature at the study site during the study period is shown in Suppl. material 2.

Autumn-winter leaf phenology of *S. canadensis* and two co-occurring natives

The leaf phenology of *S. canadensis*, *Artemisia lavandulaefolia* (Asteraceae) and *Imperata cylindrica* (Poaceae) was quantified from October 2022 to February 2023. *A. lavandulaefolia* and *I. cylindrica* are common native species co-occurring with *S. canadensis* in eastern China (Ye et al. 2019). All three species are perennial, can reproduce both sexually and asexually (clonally) by producing rhizomes and may compete intensively in the field.

In March 2022, *S. canadensis*, *A. lavandulaefolia* and *I. cylindrica* seeds were germinated in pots (5 × 5 × 6 cm) filled with a mixture of vermiculite, sand and peat (2:1:1 in volume) in a growth chamber at 24/18 °C and photosynthetic active radiation of 250 μmol·m⁻²·s⁻¹. On 8 March 2022, after two weeks, seedlings were transplanted to plots (1 × 1 m) in an open site in the experimental garden of the Institute Subtropical Forestry, Chinese Academy of Forestry in Fuyang. The open site was created by pulling out all the plants. The seedlings were planted in the centre of the plots and each plot was planted with only one seedling from one of the three species. Ten plots were established for each species (n = 10). The distribution of the three species and replicates followed a completely random design as the plots were located within a small distribution range with relatively low environmental heterogeneity. The plants were watered regularly to provide a sufficient water supply. The substrate in the plots was a type of yellow-red ferrosol (pH = 6.5 and the availability of N, P and K is 69.14 mg/kg, 0.84 mg/kg and 153.0 mg/kg,

respectively). During the growth period, the non-target plants in the plots were weeded out to prevent possible interference on the target plants.

From 5 October 2022, the beginning of autumn (mean temperature between 10 and 22 °C for five consecutive days), the number of viable old leaves (leaves on the ramets produced before the autumn) were recorded for each plant every two days. An old leaf with an estimated more than 50% of the total leaf area maintaining green colour was considered viable. The duration from the start of autumn to the day of complete senescence of the old leaves was calculated for each individual plant. On 30 November 2022, at the beginning of winter (mean temperature below 10 °C for five consecutive days), the number of new ramets (produced from the start of autumn), new leaves (appearing on the new ramets) and old viable leaves were counted for each plant. It should be noted that the leaf phenology of *S. canadensis* may vary with region, as different regions may differ greatly in their local climate. This variation in the timing of old leaf senescence and new ramet and leaf production in autumn and winter may influence the chemical control efficiency described below.

Winter photosynthetic characteristics of *S. canadensis* and *A. lavandulaefolia*

As the aboveground part of *I. cylindrica* was completely senescent in winter, photosynthetic capacities were characterised for *S. canadensis* and *A. lavandulaefolia* using the same individuals as described in the previous section. Photosynthesis was measured from 10 December to 10 February 2022, using a Li-6800 device (LI-COR, Inc., Lincoln, Nebraska). Light response curves of photosynthetic rate were measured for one old leaf and one new leaf for each of the six randomly selected plants of each species ($n = 6$). The selected old leaves were located approximately at the middle position of the old shoots and new leaves were from the rosettes of newly-produced ramets. The photosynthetic rate (A_{sat}) at the light saturation point (LSP), light compensation point (LCP), apparent quantum yield (AQY) and dark respiration rate (R_d) were calculated, based on the light response curves (Ye 2007).

Effects of glyphosate and competition on *S. canadensis* and *I. cylindrica*

The effects of glyphosate and competition on growth of *S. canadensis* and *I. cylindrica* were investigated in pot and field experiments. *S. canadensis* and *I. cylindrica* seeds were germinated and cultivated as described above. The seedlings were transplanted to pots (18 × 18 × 19 cm) filled with a mixture of silt loam soil and peat (the availability of N, P and K is 112.2 mg/kg, 1.7 mg/kg and 190.0 mg/kg, respectively) in the experimental garden.

Additive design was used to test the competitive effects of *S. canadensis* and *I. cylindrica*. One seedling of *S. canadensis* and *I. cylindrica* was grown together (with interspecific competition) or alone (without interspecific competition from each other, control) (Fig. 1). Glyphosate was applied on 5 July 2022 (two months after the start of the summer in 2022) or on January 30 (two months after the start of winter in 2022) (Fig. 1). A 20 ml glyphosate solution was applied to each plant at three levels: 0 (distilled water as control), 0.9 and 1.8 ml/l, using mini-plastic spray bottles (maximum volume: 50 ml). Glyphosate solutions were prepared by diluting the original Roundup (41% glyphosate, Monsanto Company, U.S.A)

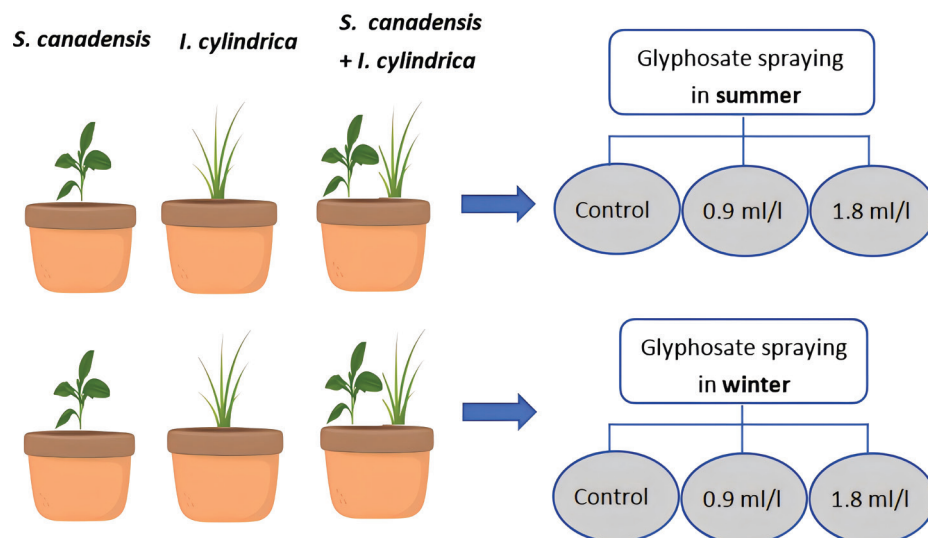


Figure 1. Overview of the experiment. Illustrations of the competition treatments (competition between invasive *Solidago canadensis* and native *Imperata cylindrica*) and the glyphosate treatments in the pot experiment in summer and winter.

with distilled water to the aforementioned concentrations. For the mixed-species pots, *S. canadensis* and *I. cylindrica* plants were temporarily separated with a plastic plate to prevent over-spraying of glyphosate. Ten replicates were performed for each competition $\times$ glyphosate treatment during each season, with a total of 90 pots (three competition treatments $\times$ three glyphosate treatments $\times$ 10 replicates) for each season. The treatments and replicates were randomly distributed and the positions of the pots were regularly re-arranged to reduce the potential effects of environmental heterogeneity in the experimental garden. The plants, treated with glyphosate in July (summer), were harvested on 5–10 November 2022 and those treated in January (winter) were harvested on 5–10 June 2023. The plants were dried at 80 °C to a constant weight and weighed to obtain dry mass.

In the field experiment, *S. canadensis* and *I. cylindrica* seedlings were cultivated in 2021 and transplanted into field plots (1 $\times$ 1 m) on 24 March 2022. The site is located at an abandoned agricultural field with a kind of red-yellow ferrosol (pH = 6.5 and the availability of N, P and K was 152.6 mg/kg, 2.3 mg/kg and 55.9 mg/kg, respectively). Two weeks before transplantation, all the plants in the plots were removed using glyphosate. A substitution design was used for the competition treatments. In the monoculture treatment, four *S. canadensis* or *I. cylindrica* plants were grown in a plot (without interspecific competition from each other). In the mixture treatment, two plants, *S. canadensis* and *I. cylindrica*, were grown in a plot (with interspecific competition). Within each plot, the plants were arranged at intervals of 50 cm. On 15 January 2022, for each species, we sprayed 120 ml of glyphosate solution (0.9 ml/l) on six randomly selected plots and 120 ml distilled water (control without glyphosate) on the other six plots. A total of 36 plots were established (three competition treatments $\times$ two glyphosate treatments $\times$ six replicates). A prior test showed that the soil physicochemical properties were relatively homogeneous between the plots and a completely random design was used in the experiment. Non-target plants were removed by pulling them out during the growth period. Four months later, on 15–17 May, the ramet number and shoot height of three randomly selected ramets in each plot were measured and the cover of *S. canadensis* and *I. cylindrica* in each plot was visually estimated.

Life forms and winter leaf phenology of co-occurring native species in the wild

The diversity of native species co-occurring with *S. canadensis* was surveyed from autumn to winter in 2023 in Shanghai City, Zhejiang Province, Jiangsu Province and Anhui Province, where it is characterised by a typical subtropical monsoon climate and *S. canadensis* has the highest distribution. We randomly selected 120 sites from these four regions, based on their latitude and longitude from these four regions. *S. canadensis* plants typically grow along roadsides, riversides or in old fields. The possible habitats of *S. canadensis* were investigated within a distance of 1 km from the centre of each site. Stands of *S. canadensis* with a patch area of $> 2 \text{ m}^2$ were found at 88 sites. A $1 \times 1 \text{ m}$ plot within each patch of *S. canadensis* and a $3 \times 3 \text{ m}$ plot outside, but closely connected to, the *S. canadensis* patch were set up. The life forms and winter leaf phenology of all plant species in the plots were recorded by observation during the site survey, as well as the description of phenology and life form in Flora of China (Editorial Committee of Flora of China 1994). Winter leaf phenology was determined another two to three times at some sites near the location of the pot experiment and the field experiment throughout the winter, if the winter phenology of some plant species could not be determined in the first survey.

Statistical analyses

One-way ANOVA was used to test the effect of species (*S. canadensis*, *A. lavandulaefolia* and *I. cylindrica*) on autumn-winter leaf phenology (duration of complete leaf senescence and the number of old leaves, new leaves and new ramets at the start of winter). The differences in photosynthetic parameters (A_{sat} , LSP, LCP, AQY and Rd) between the old and new leaves of *S. canadensis* and *A. lavandulaefolia* were also analysed using one-way ANOVA. The effects of competition, glyphosate application and their interactions were analysed using two-way ANOVA for both the pot and the field experiments. Duncan's test was used for multiple comparisons, if the effect was significant. The biomass and percentage (e.g. cover) data were log-transformed or arc-sine-transformed if they did not conform to parametric assumptions. The data illustrated in the figures and tables were not transformed. All the analyses were performed using the IBM SPSS Statistics Version 27 (IBM Corp., Armonk, New York, USA).

Results

Autumn-winter leaf phenology differences between *S. canadensis* and natives

S. canadensis differed greatly from the two co-occurring native species, *A. lavandulaefolia* and *I. cylindrica*, in terms of autumn-winter phenology (Fig. 2). From autumn to winter, the old leaves died the earliest in *I. cylindrica* and the latest in *S. canadensis* (Fig. 2A). No new ramets or leaves were present in *I. cylindrica* at the start of the winter of 2022. In contrast, new ramets and leaves were produced in *S. canadensis* and *A. lavandulaefolia* and viable, old leaves were found in these two species. The numbers of new ramets, new leaves and viable old leaves were significantly greater in *S. canadensis* than in *A. lavandulaefolia* (Fig. 2B).

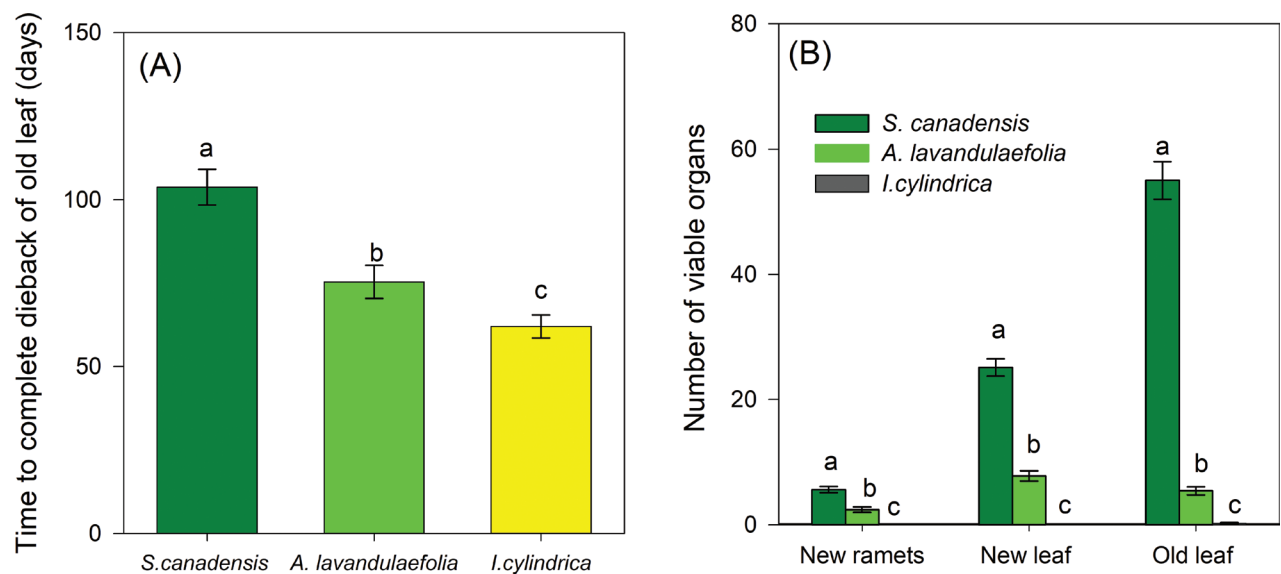


Figure 2. Winter leaf phenology of *Solidago canadensis* and the two native species (*Artemisia lavandulaefolia* and *Imperata cylindrica*) **A** time (days) to complete dieback of old leaves (the duration was calculated from the start of autumn **B** number of viable aboveground organs (new ramets, new leaves and old leaves) per plant at the start of winter. Mean $\pm$ standard error are given. Different letters indicate significant differences ($P < 0.05$).

Photosynthetic characteristics of *S. canadensis* and *A. lavandulaefolia* in winter

Both *S. canadensis* and *A. lavandulaefolia* plants were able to efficiently photosynthesise during the winter (Table 1). However, the two species differed significantly in their photosynthetic characteristics (Table 1). For both species, the new leaves had a higher photosynthetic capacity than the old leaves ($P < 0.05$). The old leaves of *S. canadensis* had a much lower LSP than those of *A. lavandulaefolia* ($P < 0.05$), although the new leaves had similar LSP ($P > 0.05$). The new leaves of *S. canadensis* had significantly higher A_{sat} than those of *A. lavandulaefolia* ($P < 0.05$). LCP and R_d were higher in the new leaves of *S. canadensis* than in those of *A. lavandulaefolia* ($P < 0.05$).

Growth responses to competition and glyphosate in *S. canadensis* and *I. cylindrica*

The growth responses of *I. cylindrica* and *S. canadensis* to glyphosate and competition varied between the two pot experiments conducted in summer and winter (Table 2). In summer, the biomass of *I. cylindrica* was significantly affected by glyphosate, competition and their interaction, whereas the biomass of *S. canadensis* was only affected by glyphosate (Table 2). In summer, the biomass of *S. canadensis* decreased by 20.1% and 59.5% in the 0.9 ml/l and 1.8 ml/l treatments, respectively, compared with the control (Fig. 3A). For *I. cylindrica*, the biomass decreased by 57.6% and 91.7% in the 0.9 ml/l and 1.8 ml/l treatments, respectively, to a much greater extent than that for *S. canadensis* (Fig. 3B). Interspecific competition significantly decreased the biomass of *I. cylindrica* in the control and the 0.9 ml/l treatments in summer, but not that of *S. canadensis* in any of the glyphosate treatments (Fig. 3A, B). In contrast, in winter, the biomass of *I. cylindrica* was hardly negatively affected by glyphosate, but was significantly affected by competition

Table 1. Photosynthetic characteristics of *Solidago canadensis* and *Artemisia lavandulaefolia* during winter.

Variable	<i>S. canadensis</i>		<i>A. lavandulaefolia</i>	
	New leaf	Old leaf	New leaf	Old leaf
LSP	960.0 ± 97.9a	533.3 ± 42.1b	963.6 ± 52.6a	810.0 ± 79.5a
A _{sat}	14.4 ± 0.7a	7.8 ± 0.6c	12.4 ± 0.3b	8.1 ± 0.4c
AQY	0.064 ± 0.002a	0.055 ± 0.002ab	0.051 ± 0.002bc	0.042 ± 0.005c
LCP	29.7 ± 4.1a	25.7 ± 2.2ab	20.0 ± 1.7b	18.2 ± 2.9b
R _d	2.0 ± 0.3a	1.5 ± 0.1b	1.2 ± 0.1bc	0.9 ± 0.1c

LSP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), light saturation point; A_{sat} ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), photosynthetic rate at LSP; AQY, apparent quantum efficiency; LCP ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), light compensation point; R_d ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), dark respiration rate. Values are presented as mean ± standard error. Different letters indicate significant differences ($P < 0.05$).

Table 2. Effects of glyphosate application and competition on *Solidago canadensis* and *Imperata cylindrica* biomass.

Season	Effect	<i>S. canadensis</i>			<i>I. cylindrica</i>		
		DF	F	P	DF	F	P
Summer	Competition	1	1.2	0.276	1	227.7	< 0.001
	Glyphosate	2	19.8	< 0.001	2	112.5	< 0.001
	Interaction	2	0.28	0.759	2	104.0	< 0.001
Winter	Competition	1	2.2	0.142	1	8.9	0.004
	Glyphosate	2	247.2	< 0.001	2	2.7	0.077
	Interaction	2	0.2	0.814	2	10.0	< 0.001

and the interaction between glyphosate and competition, whereas the biomass of *S. canadensis* was only affected by glyphosate (Table 2). In winter, the 0.9 ml/l and 1.8 ml/l glyphosate decreased the biomass of *S. canadensis* by 91.4% and 95.6%, respectively (Fig. 3C), whereas the biomass of *I. cylindrica* was not decreased significantly by the glyphosate treatments (Fig. 3D). In winter, interspecific competition did not reduce the biomass of *S. canadensis* in any of the three glyphosate treatments; however, it did reduce the biomass of *I. cylindrica* in the control and 1.8 ml/l treatments (Fig. 3C, D).

The field experiment also showed that *S. canadensis* and *I. cylindrica* differed in their responses to competition and glyphosate application during the winter (Table 3 and Fig. 4). Glyphosate application in winter reduced the shoot height, ramet density and cover of *S. canadensis*, measured in spring, by 19.9%, 48.9% and 32.1%, respectively, in the monoculture treatment and by 25.4%, 29.9% and 21.1%, respectively, in the mixture treatment (Table 3 and Fig. 4). However, glyphosate application during the winter did not significantly affect any of the spring growth measures of *I. cylindrica* (Table 3 and Fig. 4). The competition between *S. canadensis* and *I. cylindrica* negatively affected the ramet number and cover of both species. The strength of the effects of competition on ramet number seemed to be similar for the two species, but the effects on cover tended to be much stronger in *I. cylindrica* (Table 3). The growth parameters were not significantly affected by interactions between glyphosate application and competition, except for the ramet number of *S. canadensis*, which was significantly reduced by glyphosate in the monoculture treatment, but not in the mixture treatment.

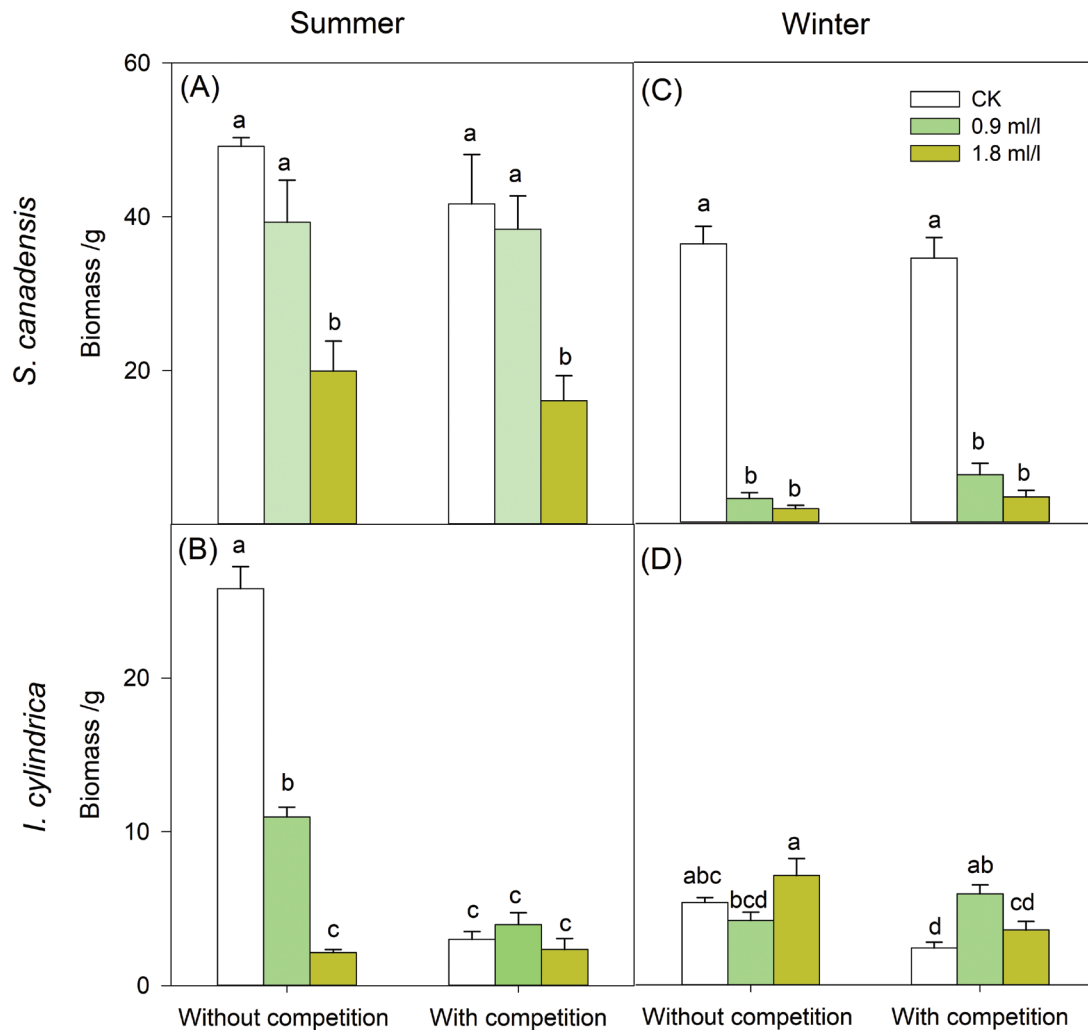


Figure 3. Biomass of *Solidago canadensis* and *Imperata cylindrica* in response to glyphosate and competition in summer and winter **A, C** invasive *S. canadensis* **B, D** native *I. cylindrica*. Glyphosate was applied at three levels: CK (distilled water, without glyphosate), 0.9 and 1.8 ml/l, with a total of 20 ml glyphosate solution for each plant in either summer (**A, B**) or winter (**C, D**). In each pot, one *I. cylindrica* or *S. canadensis* plant was grown alone (without competition) or together (with competition). Each column represents the mean $\pm$ standard error for each species. Different letters indicate significant differences ($P < 0.05$) for each treatment combination.

Table 3. Effects of glyphosate application in winter and competition on spring growth of *Solidago canadensis* and *Imperata cylindrica* in the field.

Parameter	Effect	<i>S. canadensis</i>			<i>I. cylindrica</i>		
		DF	F	P	DF	F	P
Shoot height	Competition	1	6.191	0.02	1	1.9	0.180
	Glyphosate	1	35.704	< 0.001	1	0.3	0.560
	Interaction	1	0.254	0.619	1	2.3	0.148
Ramet number	Competition	1	35.055	< 0.001	1	27.1	< 0.001
	Glyphosate	1	16.518	< 0.001	1	3.2	0.087
	Interaction	1	6.543	0.017	1	0.1	0.997
Cover	Competition	1	29.9	< 0.001	1	70.5	< 0.001
	Glyphosate	1	15.7	0.001	1	0.9	0.331
	Interaction	1	3.0	0.096	1	0.7	0.409

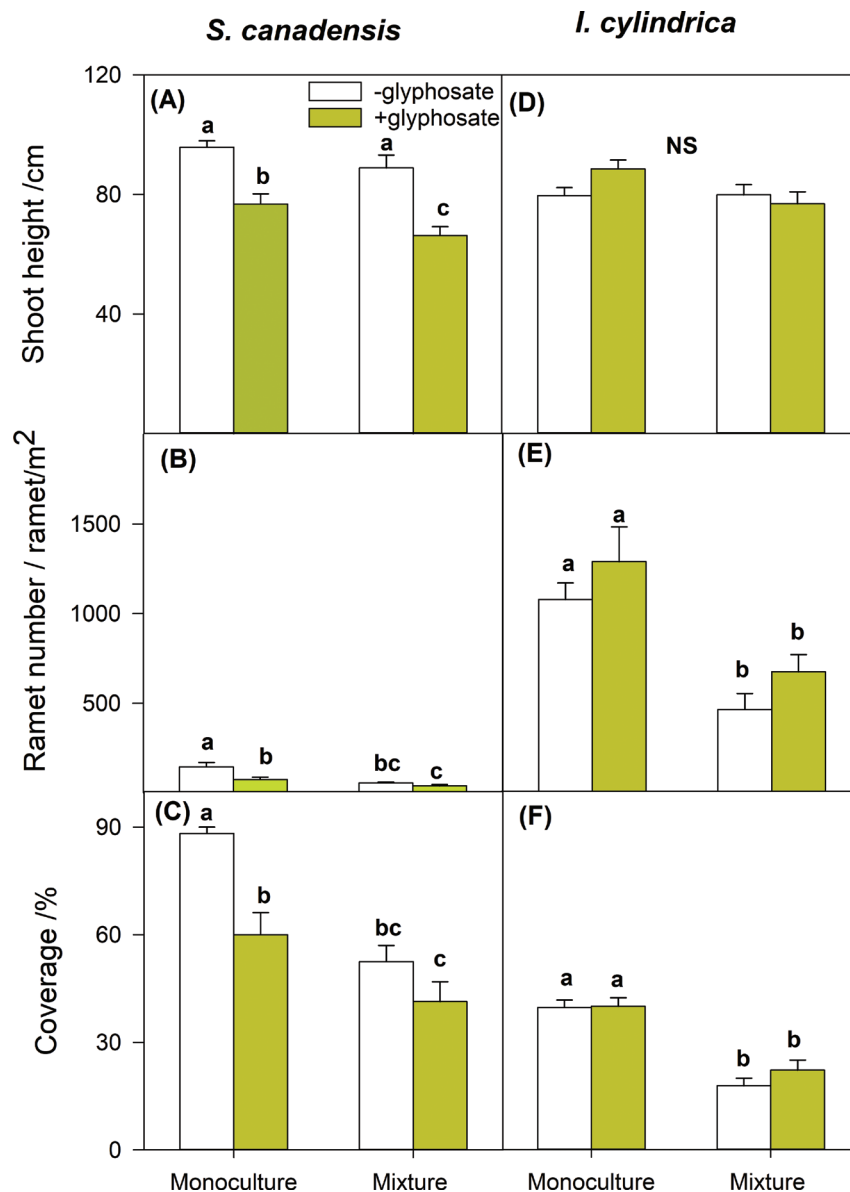


Figure 4. Spring growth of *Solidago canadensis* and *Imperata cylindrica* treated with glyphosate in winter and competition in the field. Invasive *S. canadensis* (A–C) or native *I. cylindrica* (D–F) were grown either in monoculture (without interspecific competition) or in a mixture (with interspecific competition between each other); a total of 120 ml distilled water (without glyphosate, -glyphosate) or 0.9 ml/l glyphosate solution (with glyphosate, +glyphosate) was applied to each plot. The values in the figure indicate mean $\pm$ standard error for each treatment combination. Different letters indicate significant differences ($P < 0.05$) for each growth parameter and NS indicates an insignificant difference between the treatments.

Diversity and life forms of natives co-occurring with *S. canadensis* in the wild

Native plant species that co-occurred with *S. canadensis* in the wild were divided into four groups according to their origin and life form during winter: native annuals with complete aboveground dieback, native perennials with complete leaf dieback, native perennials with viable leaves and invasive annuals with viable leaves. Only two co-occurring species, *Artemisia lavandulaefolia* and *Rumex japonicus*, had viable leaves during the winter (Table 4).

Table 4. Major co-occurring plant species of *Solidago canadensis* and their life forms.

Life forms	Leaf vitality	Major co-occurring plant species
Native annuals	Dieback	<i>Setaria viridis</i> , <i>Glycine soja</i> , <i>Lactuca indica</i> , <i>Solanum nigrum</i> , <i>Hemisteptia lyrata</i> , <i>Youngia japonica</i> , <i>Pterocypsel indica</i>
Native perennials	Dieback	<i>Phragmites australis</i> , <i>Imperata cylindrica</i> , <i>Miscanthus sacchariflorus</i> , <i>Humulus scandens</i> , <i>Pueraria lobata</i>
Native perennials	Vital	<i>Artemisia lavandulaefolia</i> , <i>Rumex japonicus</i>
Exotic annuals	Vital	<i>Erigeron philadelphicus</i> , <i>Erigeron annuus</i> , <i>Conyza canadensis</i>

Discussion

We showed that glyphosate effectively controlled photosynthetically active *S. canadensis*, a highly competitive invader, but did not affect dormant *I. cylindrica* in winter in a subtropical climate. These results support the hypothesis that glyphosate application can selectively and more efficiently depress *S. canadensis*, while avoiding harm to dormant native species, thus shifting the balance of competition towards the co-occurring native plants.

Winter phenology of *S. canadensis* and its co-occurring species

The old leaves of *S. canadensis* withered much later and produced new ramets and leaves much earlier than the two co-occurring species did. The results of the large-scale field survey also indicated that most of the co-occurring species of *S. canadensis* persisted throughout winter without viable leaves. The extension of growth period is consistent with many studies, showing that invasive species generally have longer growing seasons, which may endow them with the advantage of fixing more carbon and becoming more competitive (Wolkovich and Cleland 2011; Fridley 2012).

Temperature and/or apical dominance may control earlier vegetative growth of invasive *S. canadensis* from autumn to winter. This species begins new vegetative growth as early as early October in a subtropical climate, concurrent with the start of autumn and the flowering of *S. canadensis* (Cheng et al. 2021), when the mean maximum air temperature sharply decreases in the subtropical region (Suppl. material 1). *S. canadensis* originates from the temperate regions in North America with mild summers and the much higher air temperature in the subtropical region in eastern China may inhibit ramet production and flowering in *S. canadensis* (Cheng et al. 2021). The second explanation for the initiation of new ramet growth in autumn is that the transition from vegetative growth to flowering in *S. canadensis* releases belowground buds from apical dominance (Chung et al. 1994). The presence of apical dominance from apical buds or shoot tips inhibits the outgrowth of axillary buds located below (Cline 1997; Beveridge et al. 2023). *S. canadensis* shows a strong ability to regenerate from rhizome fragments, axillary buds and adventitious buds in stem bases or rhizomes if the aboveground part is clipped (Huang et al. 2007; Weber 2011), suggesting a strong dominance of apical buds over axillary buds and belowground parts. This apical dominance might disappear when vegetative shoots transform into inflorescences (Chung et al. 1994).

Interspecific variations in winter phenology may indicate different strategies to cope with unfavourable winter coldness in subtropical regions (Estiarte and Peñuelas 2015; Varpe 2017). Although winter is relatively mild in the region,

the extreme minimum temperature can be as low as -9°C , as recorded in early 2016. The maintenance of green leaves in *S. canadensis* during unfavourable seasons against the risk of freeze injuries indicates its high freezing tolerance, possibly owing to its origin in temperate climates with lower air temperatures in winter, as well as polyploidisation (Lu et al. 2020; Cheng et al. 2021). In contrast, most co-occurring herbaceous plant species overwinter as dormant seeds or perennial tissues (mostly underground) under subtropical conditions, representing an escape strategy (Tang et al. 2016; Varpe 2017).

It should be noted that the phenology of *S. canadensis* and its neighbours and the consequent discrepancies may vary substantially with local climate and climate change (Park et al. 2024), either through plastic phenotypic responses or evolutionary adaptations. In contrast to the autumn-winter phenology observed in this study, *S. canadensis* does not produce new ramets from rhizomes until the next spring in its native range, such as in Ontario, if undisturbed (Werner et al. 1980), likely due to much shorter growing season and relatively lower winter temperatures. Peng et al. (2019) showed that warming could extend leaf lifespan and enhance growth of *S. canadensis* and an invasive population in China was more sensitive in these responses than a native population from the USA in a common garden experiment. Cheng et al. (2021) also showed that polyploidisation improves heat tolerance and delays flowering in the invaded ranges, which may sequentially delay dieback of old shoots during the global expansion of *S. canadensis* from its temperate-climate native ranges in North America to hot-summer climate in an introduced range. These studies suggest that both plastic phenotypic and genetic changes in the invasive species may occur in response to different climate-related environments. Furthermore, studies have shown that some exotic invaders are more plastic in their responses to climate change than natives, which may increase their competitive advantages (Hulme 2011; Polgar et al. 2013) and pose challenges for future invasion management.

Effects of glyphosate application on growth and competition

This study indicates much stronger competitive capacity of *S. canadensis*, compared to that of one of its common neighbours, *I. cylindrica*, consistent with its high performance in the field (Szymura and Szymura 2016). The growth of *S. canadensis* was never reduced by competition from *I. cylindrica*, regardless of the application of glyphosate in either summer or winter. In contrast, the growth of *I. cylindrica* was almost consistently reduced by competition from *S. canadensis* in summer and in the control treatment in winter. Diverse mechanisms, including the extended growth season observed in this study, may jointly contribute to high competitiveness (Cheng et al. 2021; Wang et al. 2023; Li et al. 2024). The high competitive ability of this invader also suggests that it is not feasible to resist *S. canadensis* invasion via intensified competition from native plant species alone, without imposing further strong disturbances on the invader and simultaneously with less impact on natives, such as herbicides (Munné-Bosch and Santos 2024).

Our study suggests that chemical control of *S. canadensis* may modify the competition balance if the invader and the native neighbours are equally treated, but respond differentially to herbicides in different seasons. In summer, glyphosate may exacerbate further invasions, because *S. canadensis* is less affected and may recover more quickly than native species. *S. canadensis* was more tolerant to

glyphosate than *I. cylindrica* in summer, which was consistent with the findings of Gu et al. (2017). Invasive plant species may be more tolerant to herbicides because of their larger plant size or higher regrowth capacity (Enloe and Netherland 2017). Other studies have indicated that invasive exotic species are normally more intrinsically stress tolerant or have higher capacities to recover from disturbances or stresses (Alpert et al. 2000; Godoy et al. 2011; Wang et al. 2017, 2019, 2024; Li et al. 2022). In summer, it is also likely that temporary release of empty niches by disturbances may facilitate establishment of more targeted and non-targeted exotic invasive species.

However, winter herbicide treatment may favour native species in the long term. The ranking of tolerance to glyphosate was reversed in winter for *S. canadensis* and its neighbours. Physiological activity may play an important role in the tolerance of species to herbicides during winter. We found that, in winter, glyphosate depressed the growth of *S. canadensis*, which had viable leaves, but did not affect the growth of winter-dormant native *I. cylindrica*. These findings suggest that leaf absorption, transportation and function of herbicides depend on physiological activity of plant species at low temperatures (Devine and Bandeen 1983; Klevorn and Wyse 1984; Caplan et al. 2018). Glyphosate may still be transported downwards to the rhizomes, adventitious buds and roots of *S. canadensis* in winter, become effective belowground and impair regrowth in spring. Studies have indicated that the processes involved in herbicide functioning can be highly affected by temperature (Devine and Bandeen 1983; Klevorn and Wyse 1984). Therefore, the effects of temperature on the efficacy of *S. canadensis* control should be examined in future studies. The suppressive effects of glyphosate on the growth of *S. canadensis* were less pronounced in the field experiment than in the pot experiment, very likely due to the much larger plant size. This suggests that the application of a sufficient dosage of glyphosate or repeated annual application is essential for more efficient control of *S. canadensis* in the field.

Although the growth of *I. cylindrica* plants was strongly suppressed by the presence of *S. canadensis* when glyphosate was not applied, it accumulated equal biomass in the glyphosate treatments compared with the control treatment (without glyphosate and competition) in winter. This suggests that glyphosate alleviated the competition stresses of *S. canadensis* on *I. cylindrica*, owing to the high sensitivity of *S. canadensis* to glyphosate in winter. Unexpectedly, we did not observe any growth depression in *S. canadensis* in the presence of *I. cylindrica* in the glyphosate treatments in winter, either in the pot or field experiments. The suppression effects on the invader by natives induced by herbicide application in winter may occur only after a long period of growth recovery from the disturbances, rather than in the current short observation period, as stresses normally weaken competition intensity, which can recover if stresses recede, as predicted by the stress-gradient hypothesis (Maestre et al. 2009). Studies have shown that the effectiveness of different approaches for invasive species control has emerged at different times (Mahmood et al. 2018), indicating that studies with realistic treatments at large timescales are important for understanding control effects (Sherrill et al. 2022). Therefore, future studies should focus on the long-term effects of spraying glyphosate and other herbicides on *S. canadensis* during winter.

One caveat is that we recorded two winter active native forbs, *A. lavandulaefolia* and *R. japonicus*. Although these forbs sometimes grow together with *S. canadensis*, unlike most winter-dormant grass species, they normally have distinct spatial separa-

tion from *S. canadensis*, indicating mutual exclusion of these phenologically similar species. Therefore, they are less likely to be injured if herbicide drift is minimised. On the other side, common winter dormant grasses, such as *P. australis*, *I. cylindrica* and *M. sacchariflorus*, tend to form large monocultural patches and are readily replaced by *S. canadensis* (Ye et al. 2019). In the early and middle stages of invasion, herbicide application in winter can selectively control the invader while protecting these dormant natives, which may reverse the succession direction and promote restoration of native cover. The efficiency of winter application of glyphosate and other herbicides in controlling *S. canadensis* while promoting restoration of diverse native plant cover should be examined under the subtropical climate conditions in the future.

We conclude that contrasting winter leaf phenology of the invasive *S. canadensis* and co-occurring native species provides the opportunity to control *S. canadensis* with glyphosate in winter, resulting in higher herbicide selectivity and efficiency under the subtropical climatic conditions. The principles behind this approach may be generally applicable in situations where invasive plant species and their co-occurring native species show distinct phenological niche separations.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualisation, X.Y, M.W, R.Z and F.Y; methodology, X.Y.; data curation and investigation, X.Y, J.M, J.L and R.M.; writing—original draft preparation, X.Y; writing—review and editing, X.Y, M.W, R.M. and F.Y; supervision, M.W. and F.Y.; project administration, X.Y. and M.W.; funding acquisition, X.Y. and M.W. All the authors have read and agreed to the published version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

The mean daily maximum air temperature, mean daily minimum air temperature and mean monthly precipitation of Fuyang, Hangzhou over the last ten years (2014–2023)

Authors: Xiaoqi Ye, Jinliu Meng, Ruixiang Ma, Jili Liang, Ming Wu, Rongzhou Man, Feihai Yu

Data type: tif

Explanation note: The data were edited from the China Meteorological Data Service Center (<http://data.cma.cn/>).

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Link: <https://doi.org/10.3897/neobiota.96.129863.suppl1>

Supplementary material 2

Mean daily air temperature of Fuyang, Hangzhou from 1 March 2022 to 28 February 2023

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Data type: tif

Explanation note: The data were edited from China Meteorological Data Service Center (<http://data.cma.cn/>).

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