INTRODUCTION

The success of invasive plants can be ascribed to a suite of contributors. Mounting evidence suggests that plant phenology may play a pivotal role in driving plant invasions (Fridley, 2012; Godoy, Castro-Diez, Valladares, & Costa-Tenorio, 2009; Novy, Flory, & Hartman, 2013; Rejmánek, 2013; Smith & Hall, 2016; Smith & Reynolds, 2015; Wolkovich & Cleland, 2011). Harrington, Brown, and Reich (1989) pioneered work in this aspect, and their research has brought renewed interest in the study of plant phenology (Cleland, Chui, Menzel, Mooney, & Schwartz, 2007). Overall, invasive plants occupy unique phenological niches that confer them with growth or competitive advantages over native species (Fridley, 2012; Wolkovich & Cleland, 2011; Wolkovich et al., 2013). For example, invasive plants commonly exhibit extended leaf phenology, which grants them longer intervals between leaf budbreak in spring and abscission in autumn relative to co-occurring natives and allows them to exploit light and nutrients unavailable to dormant natives (Fridley, 2012; Rejmánek, 2013; Wolkovich & Cleland, 2011). Some invaders also have extended flowering and fruiting phenology (Rejmánek, 2013). Additionally, phenological plasticity of an invader may be related to its invasiveness potential (Godoy et al., 2009).
The need to study phenology in plant invasions has become widely recognized, but several aspects remain to be poorly understood. First, the majority of phenological studies have been conducted in temperate or alpine climates primarily because these regions have long been viewed to be temperature-sensitive (e.g., Fridley, 2012; Harrington et al., 1989; Smith, 2013). As such, information is quite limited about the role of phenology in plant invasions under tropical or subtropical climates. Second, previous studies have mainly focused on spring-flowering plants (Godoy et al., 2009; Smith, 2013; Wolkovich & Cleland, 2011; Wolkovich et al., 2013), and therefore, it is poorly known about the phenology of autumn-flowering plants. Third, most studies have concentrated on one or two phenological phases but not on phenological sequences (but see Fernandes, Antunes, Correia, & Mágua, 2015). In fact, phenological sequences are more important than single phenological events in understanding the ecological roles of plant phenology (Fernandes et al., 2015; Post, Pedersen, Wilmers, & Forchhammer, 2008; Zhang, Post, & Shea, 2012).

Plant phenology is strongly driven by climate, and temperature is the most important driver of plant phenology (Lieth, 1974). Climate warming profoundly influences plant phenology (Cleland, Chiariello, Loarie, Mooney, & Field, 2006; Gerst, Rossington, & Mazer, 2017; Godoy et al., 2009; Hovenden, Wills, Schoor, Williams, & Newton, 2008; Novy et al., 2013), and invasive plants track climate warming more closely than native plants (Wolkovich et al., 2013). Aside from climate warming, atmospheric nitrogen (N) deposition is also among the key components of global change (Galloway et al., 2004). N deposition is likely to be serious in some regions invaded by exotic plants because N deposition and plant invasions occur at the same time in many cases. Cleland et al. (2006) found that N deposition delayed the flowering of grasses and slightly accelerated the flowering of forbs. In addition, plant community types affect plant phenology (Elzinga et al., 2007; Lieth, 1974), although this aspect has been overlooked (Dorji et al., 2013; Hüblter, Bardy, & Dullinger, 2011). Similarly, invasion stages might influence the phenology of exotic plants. No studies to date have explicitly addressed the joint effects of climate warming, N deposition, and invasion stages on the phenology of plant invaders.

_Solildago canadensis_ is a serious invader worldwide so that it has received increasing attention (Dong, Lu, Zhang, Chen, & Li, 2006). However, it should be noted that limited efforts have been paid to the impacts of global change on its phenology. Here, we did not consider its leaf phenology because the leaves of _S. canadensis_ can emerge and die throughout a year in a subtropical climate. Reproduction is among the most important life history events (Harper, 2010). In general, reproductive phenology mainly includes the emergence of flower buds or inflorescence, flowering, and fruiting. These processes determine the quantity and quality of sexual propagules (Harper, 2010). Dieback is an important factor in determining growing season length (Li, Shao, Qiu, & Li, 2013). There has been little information about the dieback phenology of invasive plants and its ecological consequences (but see Li et al., 2009).

The purpose of this study was to understand the phenological sequences (i.e., first inflorescence buds, flowering, seed-setting, and dieback) of autumn-flowering invasive species under a subtropical climate in response to climate warming, N deposition, and invasion stages. To do so, we conducted a field experiment with _S. canadensis_ and observed its four phenophases. Specifically, we focused on the following questions. How do experimental warming, N-addition, and plant community types influence the phenological sequences of _S. canadensis_? Are the first inflorescence buds, flowering, seed-setting, and dieback correlated with invasion success?

### 2 MATERIALS AND METHODS

#### 2.1 Study species and experimental garden

_Solildago canadensis_, a worldwide invasive plant native to North America, has invaded several provinces in southeastern China and is expanding rapidly (Dong et al., 2006). Once established successfully, _S. canadensis_ could form near or complete monocultures in invaded habitats, such as roadsides, abandoned fields, agricultural fields, and pastures. In its home range, the inflorescence of _S. canadensis_ is first evident in late July or early August (Werner, Bradbury, & Gross, 1980). However, in its invaded range in China, it doesn’t start flowering until September. In our experiment, the seeds of _S. canadensis_ were collected by hand from its 30 individuals in Ningbo, Zhejiang Province, a region invaded by it seriously, in 2011. These individuals had relatively similar genotypes because they were from the same plant community.

We also selected four native species (i.e., Carex tristachya, Elymus dahuricus, Poa pratensis, and Solidago decurrens) to assemble a native plant community. These four species were selected for the following reasons: they are common species in the invaded areas in China, and their congeners are also common in North America where _S. canadensis_ is native.

To do this research, we established a common garden at Chengdu University of Technology (30.67°N, 104.06°E, and 512 m above sea level) in 2012. The garden was very flat and roughly occupied an area of 10 m × 20 m (Figure 1); it was characterized by mean annual

![Figure 1](image.jpg) An image of the experimental garden and warming manipulation in 2012. Photograph credit: Y. Peng
precipitation of 918 mm and mean annual temperature of 16.2°C (1970–2000), and ferralsol. Climatically, this experimental garden was located in a subtropical region.

2.2 | Experimental designs

We conducted a factorial field experiment at our common garden to answer the above-mentioned questions. Three factors were warming, N-addition, and community type, each with two levels. As suggested above, these factors are important drivers of plant phenology and their roles have been overlooked. Each experimental manipulation was replicated eight times, yielding 64 mesocosms (2 community types x 2 warming levels x 2 N levels x 8 replicates = 64 mesocosms). In April 2012, we collected local topsoil from several abandoned fields at Chengdu University of Technology, sifted all soils free from rocks, and mixed them with sand (1:1 volume) thoroughly. This procedure could allow soil properties (e.g., soil microbes and nutrients) to be relatively homogenous. The homogenized soil was filled into 64 mesocosms (30 cm length x 30 cm width x 20 cm depth) with 16 10-mm meshes at the bottom.

All plant assemblages were from seed. In early June 2012, 32 mesocosms were sown with S. canadensis seeds only to generate monocultures (analogous to late invasion stages), and the rest were sown with the seeds of C. trisnachya, E. dahuricus, P. pratensis, S. canadensis, and S. decurrens to generate mixtures (analogous to early invasion stages). Seedlings were thinned gradually after seed germination and finally, only four seedlings per species occurred in each mesocosm. Accordingly, plant community types covered monocultures and mixtures, representing two typical communities invaded by S. canadensis in the field.

All the warming mesocosms were heated with a MSR-2420 infrared radiator (Kalglo Electronics, Bethlehem, PA, USA) that was suspended 1.5–2.0 m above the soil surface during the experiment, roughly increasing air temperatures by 2°C (see below for details). This increase in air temperature was chosen according to the range projected by previous studies (IPCC, 2015; Meinshausen et al., 2009). For each unwarmed mesocosm, one “dummy” heater with the same shape and size was hanged as the infrared radiator to simulate the shading effect of the infrared radiator. Year-round warming has been lasting since June 2012. We placed two data loggers (HOBO Pro v2) above community canopy under ambient and warming conditions, respectively. In other words, all data loggers were suspended at the same height. We recorded air temperatures at 5-min intervals during the experiment.

Ammonium nitrate (NH₄NO₃) was selected as N source because it has been widely used in previous studies simulating N deposition. According to the previous predictions for future N deposition rates (Galloway et al., 2004), we used 4 g N m⁻² year⁻¹ as N-addition rate. Specifically, N deposition was simulated by surface applications totaling 4 g N m⁻² year⁻¹; 1 g N m⁻² was added in a wet pulse in March, April, May, and June each year. Meanwhile, the same amount of water was supplied to the mesocosms without N-addition.

We weeded and supplied water to each mesocosm as necessary (e.g., the presence of obvious drought) during the course of the experiment. We monitored S. canadensis individuals per mesocosm and observed the onset of their first inflorescence buds, flowering, seed-setting, and dieback from September to January of the subsequent year. The onset of inflorescence buds, flowering, seed-setting, and dieback was defined as the presence of first inflorescence buds, open flowers, seed maturation, and dead shoots in each mesocosm, respectively. These phenophases were chosen for the following reasons: They are ecologically important and practically feasible, and different observers can identify them accurately. All phenological observations were implemented every 1–3 days, and these observations lasted from September 2014 to January 2017. From these observations, we separately determined the number of days from 1 January (i.e., day of year, DOY) for each phenological phase in each mesocosm. Note that the dieback of S. canadensis occurred in January of the subsequent calendar year so that the DOY for first dieback was calculated as the number of days from 1 January of the previous year. Therefore, the DOY values for dieback were greater than 365. Additionally, we surveyed ramet numbers and height in each mesocosm in late September, both of which can to some extent indicate invasion success.

2.3 | Statistical analyses

We used a one-way analysis of variance (ANOVA) to test whether mean air temperatures differed among three years or to test whether the phenological phases of S. canadensis monocultures grown under the ambient conditions differed among three years. Second, we used paired t-test to test the warming effect on air temperatures. Third, a four-way ANOVA was used to test the effects of experimental warming, N-addition, community type, year, and their interactions on the phenology of S. canadensis. Finally, a model II regression was used to test the relationships between invasion success (i.e., ramet number and height) and each phenological phase. A model II regression was chosen as invasion success and phenophase were random variables and they were not mutually independent. All the ANOVAs and t-test were carried out with SPSS 19.0 (SPSS Inc., Chicago, IL, USA), and a model II regression was performed using the package “smatr” (R Development Core Team, 2016).

3 | RESULTS

During the four phenophases of S. canadensis, the mean air temperatures under ambient conditions fluctuated from 14.1°C in 2014 to 15.3°C in 2016, but did not differ among three years (Figure 2a). Meanwhile, the precipitation was 143, 374, and 181 mm for 2014, 2015, and 2016 over that time period. For S. canadensis monocultures grown under the ambient conditions, the onset of first inflorescence buds (Figure 2b), flowering (Figure 2c), and seed-setting (Figure 2d) shifted with years significantly. In contrast, the onset of first dieback retained unchanged with years (Figure 2e).
Heating manipulations significantly increased air temperatures by 2.7°C in 2014, 1.9°C in 2015, and 1.7°C in 2016. Warming influenced the onset of first inflorescence buds, flowering, seed-setting, and dieback; in contrast, N-addition did not influence these four phenophases (Table 1). Plant community types influenced the onset of first seed-setting rather than the other three phenophases (Table 1). Four phenophases varied with year significantly (Table 1; Figure 3a–d). Additionally, the interannual shifts in first seed-setting and dieback were tightly dependent on plant community types (Table 1: interactive effects between year and community type; Figure 3c,d).

N-addition did not affect *S. canadensis* phenology, but it modified the warming effect on seed-setting (Table 1: interactive...
The first seed-setting date of *S. canadensis* was 1.6 days earlier when it was grown alone than when it was grown with four natives (Table 1: effect of type; Figure 3c). The presence of natives also strongly modified the warming effect on seed-setting (Table 1: interactive effect between warming and type). That is, warming delayed the first seed-setting date of *S. canadensis* by 2.4 days when it was grown alone but did not influence this date when it was grown with natives (Figure 3c).

Across three years, experimental warming delayed the first inflorescence date by 1.3 days (Figure 4a), first flowering date by 1.4 days (Figure 4b), first seed-setting date by 1.5 days (Figure 4c), and first dieback date by 1.2 days (Figure 4d) of *S. canadensis*. Taken together, 2°C climate warming might significantly delay these four phenophases of *S. canadensis*.

The total number of ramets per mesocosm was uncorrelated with the onset of first inflorescence buds (Figure 5a: $p > 0.05$), first flowering (Figure 5b: $p > 0.05$), first seed-setting (Figure 5c: $p > 0.05$), and first dieback (Figure 5d: $p > 0.05$). The height of ramets was marginally or significantly correlated with the onset of first inflorescence buds (Figure 5e: $p < 0.1$), first flowering (Figure 5f: $p < 0.05$), and first seed-setting (Figure 5g: $p < 0.1$), but not first dieback (Figure 5h: $p > 0.05$). Thus, reproductive phenology could indicate invasion success, as measured by ramet height.
Under ambient conditions, the first inflorescence buds, flowering, seed-setting, and dieback of *S. canadensis* showed contrasting interannual patterns (Figure 2). These patterns suggest that plant phenological changes may be attributable to other factors than temperature and precipitation, and also support the traditional viewpoint that the factors determining plant phenology are diverse and complex (Lieth, 1974). For example, population size and photoperiod can alter plant phenology (Kouressy, Dingkuhn, Waksman, & Heinemann, 2008; Tooke & Battey, 2010). Although soil microbes and genotypes can also influence plant phenology (Kouressy et al.,...
2008; Wagner et al., 2014), their role might be highly limited in this study due to the fact that experimental soils were homogenized and S. canadensis seeds were collected from the same plant community.

We found that experimental warming, N-addition, and community types differentially influenced the phenology of S. canadensis, and they exhibited interactive effects on the first seed-setting but not the other three phenophases (Figure 3). Our findings also highlight that S. canadensis might be sensitive to 2°C climate warming and insensitive to the current N deposition rates (i.e., 4 g N m⁻² year⁻¹).

Around 2°C warming caused the delayed onset of first inflorescence buds, flowering, seed-setting, and dieback of the autumn-flowering invader S. canadensis (Figure 4). Similar phenomenological delays due to climate warming have been detected in some spring-flowering plants (Fitter & Fitter, 2002; Menzel et al., 2006). These delays in reproductive phases could be commonly attributed to the fact that warming delays the fulfillment of chilling requirements and thus leads to a later onset of reproduction (Yu, Luedeling, & Xu, 2010 and references therein). Similarly, the delayed dieback due to warming could be ascribed to antecedent heat regimes, mainly temperatures of the preceding months (Badeck et al., 2004). The delayed dieback implies that warming could, to some extent, extend growing season length. Although climate warming influenced the performance of invasive and native plant species at the same time, it favored the colonization by invasive species over native species (Gillard, Thiebaut, Rossignol, Berardocco, & Deleu, 2017). Additionally, warming scenarios and magnitudes had differential effects on the performance of invasive and native plant species (Chen, Gao, Liao, & Peng, 2017).

Unlike our findings, Cleland et al. (2006) found that an addition of 7 g N m⁻² year⁻¹ significantly influenced the phenology of grasses and forbs. Therefore, the dose of N-addition seems to matter in altering plant phenology. We also found that the delayed seed-setting due to warming was evened out by N-addition or the presence of native plants. More recently, Wan et al. (2017) reported that N availability regulated the effects of phosphorus on S. canadensis and Valliere, Irvine, Santiago, and Allen (2017) reported N availability modulated the effects of drought on native and nonnative species. Here we put forward a possibility for our finding. Warming enhanced the growth of S. canadensis, thereby speeding up soil N depletion; N-addition could slow down this depletion directly, and the presence of native plants could slow down this depletion indirectly due to their slower growth (personal observations). Taken together, our findings highlight the importance of soil N availability in regulating the warming effects on some phenological events. Although an addition of 4 g N m⁻² year⁻¹ did not alter the phenology of S. canadensis directly, our findings might help us to understand how soil N availability influences the phenology of autumn-flowering plants in the context of climate warming.

The most novel finding of our study was that the first seed-setting date of S. canadensis was earlier in monocultures than in mixtures. We propose a hypothesis for this phenomenon. In mixtures, the overall growth of a plant community was relatively slower, depleting soil nutrients slowly; in contrast, the overall growth of a plant community was relatively faster in monocultures, depleting soil nutrients faster. Thus, the phenological shifts with community types might be closely linked to differential soil nutrient depletions. To date, information is limited about how biotic factors influence plant phenology (Elzinga et al., 2007; Wagner et al., 2014). This is especially true for invasive plants. In a general sense, mixed plant communities can roughly represent early invasion stages, and plant monocultures can represent late invasion stages. Our findings suggest that the onset of S. canadensis seed-setting occurs later at early invasion stages than at late invasion stages. Although this shift did not occur in the first inflorescence buds, flowering, and dieback, this study provides evidence that some phenological phases of plant invaders may shift with invasion stages. In North America, S. canadensis inflorescence buds emerge in late July or early August (Werner et al., 1980); in China, their emergence occurs in mid- or late September (Dong et al., 2006). Such a shift between home versus invaded ranges appears to be related to invasiveness.

Reproductive phenology could, to some extent, indicate the invasion success of S. canadensis. When ramet height was chosen as a proxy of invasion success, it was associated with the onset of first inflorescence buds, flowering, and seed-setting (Figure 5). In other words, reproductive phenology contributed to invasion success. In contrast, there were no relationships between invasion success and reproductive phenophases when ramet numbers were used as a proxy of invasion success (Figure 5). In the field, S. canadensis is a typical clonal plant, has a strong capacity to yield offspring asexually, and ramet numbers are primarily determined by clonal growth (Dong et al., 2006; Werner et al., 1980). This clonality confers competitive advantages to S. canadensis and thus contributes greatly to its invasion success (Dong et al., 2006). This viewpoint is consistent with our recent field observations (Wei-Ming He, Li-Jia Dong, & Hong-Wei Yu, unpublished data). Meanwhile, this clonality might help to explain why ramet numbers were not correlated with reproductive phenology. Note that the nature of ramet growth is vegetative growth (i.e., clonal growth), which is tightly linked to biomass accumulation over the growth period. In this sense, the production of ramets may be closely associated with growth season length. As discussed above, warming could expand growth season and thus might enhance ramet production. Importantly, S. canadensis can yield new leaves throughout a year, which might be beneficial for its individuals to accumulate biomass. Our data also highlight that it is important to distinguish sexual and asexual reproduction when addressing the role of phenological sequences in driving plant invasions.

Plant phenology is a key aspect of life history strategies to cope with changing environments (Chuine & Régnière, 2017). This study advances our understanding of the effects of climate warming, N deposition, and invasion stages on the phenological sequences of autumn-flowering invaders in a subtropical climate. Briefly, symmetric 2°C climate warming might delay the phenology of autumn-flowering invaders. The current N deposition rates might not influence the phenology of autumn-flowering invaders. Among the four phenophases observed, seed-setting was most sensitive to manipulations. Thus, this phenophase appears to be a good indicator of global change. Importantly, our findings provide primary evidence...
that phenological cues may have payoffs for plant invaders. Invasion stages might influence the phenology of plant invaders, and the reproductive phenology of invaders might be linked to their invasion success.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

W.M.H., P.H.P., and J.J.L. designed the experiment. Y.P., J.X.Y., and X.H.Z. performed the experiment and collected the data. Y.P., J.X.Y., and W.M.H. analyzed the data. W.M.H., Y.P., and J.X.Y. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ORCID

Wei-Ming He https://orcid.org/0000-0002-2655-8438

REFERENCES

Badeck, F. W., Bonneau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J., & Sitch, S. (2004). Responses of spring phenology to climate change. New Phytologist, 162, 295–309. https://doi.org/10.1111/j.1469-8137.2004.01059.x

Chen, B., Gao, Y., Liao, H., & Peng, S. (2017). Differential responses of invasive and native plants to warming with simulated changes in diurnal temperature ranges. AoB PLANTS, 9, px028.

Chuiine, I., & Régnière, J. (2017). Process-based models of phenology for plants and animals. Annual Review of Ecology, Evolution, and Systematics, 48, 159–182. https://doi.org/10.1146/annurev-ecolsys-110316-022706

Cleland, E. E., Chiariello, N. R., Loarie, S. R., Mooney, H. A., & Field, C. B. (2006). Diverse responses of phenology to global changes in a grassland ecosystem. Proceedings of the National Academy of Sciences of the United States of America, 103, 13740–13744. https://doi.org/10.1073/pnas.0600815103

Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A., & Schwartz, M. D. (2007). Shifting plant phenology in response to global change. Trends in Ecology & Evolution, 22, 357–365. https://doi.org/10.1016/j.tree.2007.04.003

Dong, M., Lu, J., Zhang, W., Chen, J., & Li, B. (2006). Canada goldenrod (Solidago canadensis): An invasive alien weed rapidly spreading in China. Acta Phytotaxonomica Sinica, 44, 72–85. https://doi.org/10.1360/aps050068

Dorji, T., Totland, Ø., Moe, S. R., Hopping, K. A., Pan, J., & Klein, J. A. (2013). Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. Global Change Biology, 19, 459–472. https://doi.org/10.1111/gcb.12059

Elzinga, J. A., Atlan, A., Biere, A., Gigord, L., Weis, A. E., & Bernasconi, G. (2007). Time after time: Flowering phenology and biotic interactions. Trends in Ecology & Evolution, 22, 432–439. https://doi.org/10.1016/j.tree.2007.05.006

Fernandes, P., Antunes, C., Correia, O., & Mágua, C. (2015). Do climatic and habitat conditions affect the reproductive success of an invasive tree species? An assessment of the phenology of Acacia longifolia in Portugal. Plant Ecology, 216, 343–355. https://doi.org/10.1007/s11258-014-0441-9

Fitter, A. H., & Fitter, R. S. R. (2002). Rapid changes in flowering time in British plants. Science, 296, 1689–1691. https://doi.org/10.1126/science.1071617

Fridley, J. D. (2012). Extended leaf phenology and the autumn niche in deciduous forest invasions. Nature, 485, 359–362. https://doi.org/10.1038/nature1056

Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., … Vörösmarty, C.J. (2004). Nitrogen cycles: Past, present, and future. Biogeochemistry, 70, 153–226. https://doi.org/10.1007/s10533-004-0370-0

Gerst, K. L., Rossington, N. L., & Mazer, S. J. (2017). Phenological responsiveness to climate differs among four species of Quercus in North America. Journal of Ecology. https://doi.org/10.1111/1365-2745.12774

Gillard, M., Thiebaut, G., Rossignol, N., Berardocco, S., & Deleu, C. (2017). Impact of climate warming on carbon metabolism and on morphology of invasive and native aquatic plant species varies between spring and winter. Environmental and Experimental Botany, 144, 1–10. https://doi.org/10.1016/j.envex.2017.09.009

Godoy, O., Castro-Diez, P., Valladares, F., & Costa-Tenorio, M. (2009). Different flowering phenology of alien invasive species in Spain: Evidence for the use of an empty temporal niche? Plant Biology, 11, 803–813. https://doi.org/10.1111/j.1438-6767.2008.00185.x

Harper, J. L. (2010). Biology of plant populations. Caldwell, NJ: Blackburn Press.

Harrington, R. A., Brown, B. J., & Reich, P. B. (1989). Ecophysiology of exotic and native shrubs in southern Wisconsin: I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. Oecologia, 80, 356–367. https://doi.org/10.1007/BF00379037

Hovenden, M. J., Wills, K. E., Schoor, J. K. V., Williams, A. L., & Newton, P. C. D. (2008). Flowering phenology in a species-rich temperate grassland is sensitive to warming but not elevated CO₂. New Phytologist, 178, 815–822. https://doi.org/10.1111/j.1469-8137.2008.02419.x

Hübl, K., Bardy, K., & Dullinger, S. (2011). Effects of snowmelt timing and competition on the performance of alpine snowbed plants. Perspectives in Plant Ecology, Evolution & Systematics, 13, 15–26. https://doi.org/10.1016/j.ppees.2011.01.001

IPCC (2015). Climate change 2014: Synthesis Report. Geneva, Switzerland: IPCC.

Kouressy, M., Dingkuhn, M., Waksman, M., & Heinemann, A. B. (2008). Adaptation to diverse semi-arid environments of sorghum genotypes having different plant type and sensitivity to photoperiod. Agricultural and Forest Meteorology, 148, 357–371. https://doi.org/10.1016/j.agrformet.2007.09.009

Li, H., Shao, J., Qiu, S., & Li, B. (2013). Native Phragmites dieback reduced its dominance in the salt marshes invaded by exotic Spartina in the Yangtze River estuary, China. Ecological Engineering, 57, 236–241. https://doi.org/10.1016/j.ecoleng.2013.04.033

Li, H., Zhi, Y., An, S., Zhao, L., Zhou, C., Deng, Z., & Gu, S. (2009). Density-dependent effects on the dieback of exotic species Spartina anglica in coastal China. Ecological Engineering, 35, 544–552. https://doi.org/10.1016/j.ecoleng.2008.03.001
Lieth, H. (1974). *Phenology and seasonality modeling*. Berlin, Germany: Springer Verlag. https://doi.org/10.1007/978-3-642-51863-8

Meinshausen, M., Meinshausen, N., Hare, W., Raper, S. C. B., Frieler, K., Knutti, R., … Allen, M. R. (2009). Green-house-gas emission targets for limiting global warming to 2°. *Nature*, 458, 1158-1162. https://doi.org/10.1038/nature08017

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., … Briede, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12, 1969-1976. https://doi.org/10.1111/j.1365-2486.2006.01193.x

Novy, A., Flory, S. L., & Hartman, J. M. (2013). Evidence for rapid evolution of phenology in an invasive grass. *Journal of Evolutionary Biology*, 26, 443-450. https://doi.org/10.1111/jeb.12047

Post, E. S., Pedersen, C., Wilmers, C. C., & Forchhammer, M. C. (2008). Phenological sequences reveal aggregate life history response to climatic warming. *Ecology*, 89, 363–370. https://doi.org/10.1890/06-2138.1

Rejmánek, M. (2013). Extended leaf phenology: A secret of successful invaders? *Journal of Vegetation Science*, 24, 975–976. https://doi.org/10.1111/jvs.12116

Smith, L. M., & Hall, S. (2016). Extended leaf phenology may drive plant invasion through direct and apparent competition. *Oikos*, 125, 839–848. https://doi.org/10.1111/oik.02529

Smith, L. M., & Reynolds, H. L. (2015). Extended leaf phenology, allelopathy, and inter-population variation influence invasion success of an understory forest herb. *Biological Invasions*, 17, 2299–2313. https://doi.org/10.1007/s10530-015-0876-5

Wan, L., Qi, S., Zou, C. B., Dai, Z., Zhu, B., Song, Y., & Du, D. (2017). Phosphorus addition reduces the competitive ability of the invasive weed *Solidago canadensis* under high nitrogen conditions. *Flora*, 240, 68–75.

Yu, H., Luedeling, E., & Xu, J. (2010). Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 22151–22156. https://doi.org/10.1073/pnas.1012491107

Zhang, R., Post, E., & Shea, K. (2012). Warming leads to divergent responses but similarly improved performance of two invasive thistles. *Plant Ecology*, 54, 583–589.