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Warming during maternal generations delays offspring germination in native and nonnative species

Meredith A. Zettlemoyer and Jennifer A. Lau

M. A. Zettlemoyer (https://orcid.org/0000-0002-8203-7207) ✉ (meredith.zettlemoyer25@uga.edu) and J. A. Lau, Kellogg Biological Station, Michigan State Univ., Hickory Corners, MI, USA; and: Dept of Plant Biology, Michigan State Univ., East Lansing, MI, USA. MAZ also at: Dept of Plant Biology, Univ. of Georgia, Athens, GA, USA. JAL also at: Dept of Biology & Environmental Resilience Inst., Indiana Univ., Bloomington, IN, USA.

As environmental conditions shift due to global warming and other human-caused environmental changes, plastic responses in phenological traits like germination or flowering time may become increasingly important. While phenological plasticity is a common response to global warming, with many populations exhibiting earlier germination or flowering in warmer years, warming may also result in transgenerational plasticity, especially on early life stages. In other words, seeds produced by mothers inhabiting warmer environments may germinate faster (or slower) than seeds produced by mothers inhabiting ambient or cooler environments. Here, we use seeds collected from a field warming experiment to examine how germination and early growth differ in response to ambient versus warmed (+3°C) temperatures experienced by both maternal and offspring generations. Because nonnative species are often more phenotypically plastic than native species and because a variety of life-history traits and environmental factors affect the evolution of both within- and transgenerational plasticity, we include multiple invasive and native plant species in our study. On average, warming experienced during maternal generations delayed germination by ~0.2 days °C^{-1}, although species varied in the magnitude of response. In contrast, warming during the offspring generation tended to advance germination by ~0.1 days °C^{-1}. Nonnative species demonstrated higher germination success than native species, but we detected no differences in germination timing between native and nonnative species or that native and nonnative species differed in either within- or transgenerational plasticity, although species (independent of native status) did exhibit differing degrees of within- and transgenerational plasticity in germination timing and early growth. This study suggests that temperatures experienced by maternal plants can influence their offspring's germination phenology, potentially even more so than temperatures experienced in the offspring's immediate environment.

Keywords: biological invasions, climate change, germination, maternal effects, plasticity

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Introduction

Phenotypic plasticity (i.e. the ability to vary in phenotype under different environmental conditions; Pigliucci 2008) may allow species to express advantageous phenotypes across a broad range of environmental conditions (Baker 1965). Because phenotypic plasticity is a major response to global warming, it potentially contributes to species success under future environmental conditions (Matesanz et al. 2010, Merilä and Hendry 2014). For instance, increased allocation to root mass increases water acquisition under drought (Sultan and Bazzaz 1993, Heschel et al. 2004), and advancing phenology under increasing temperature or nutrient availability can help many plants escape stressful conditions or increase reproduction (Cohen 1976, Menzel et al. 2006, Power et al. 2006, Franks et al. 2007, Gugger et al. 2015, Lustenhouwer et al. 2017). Thus, (within-generational) plastic responses may be beneficial for plant performance under changing environments and reduce potential fitness consequences of global change (Hendry et al. 2008, Nicotra et al. 2010, Lázaro-Nogal et al. 2015).

Transgenerational plasticity (i.e. the influence of the parental generation's environment on offspring phenotypes), like within-generational plasticity, can affect fitness (survival and fecundity) (Uller 2008, Snell-Rood 2013, Vayda et al. 2018) and population persistence (Donelan et al. 2020). For example, transgenerational plasticity increases desiccation tolerance in dog ticks (Yoder et al. 2006), drought tolerance in *Impatiens capensis* and *Polygonum persicaria* (Riginos et al. 2007, Sultan et al. 2009, Herman and Sultan 2011, Herman et al. 2012), thermal tolerance in minnows and sticklebacks (Salinas and Munch 2012, Shama and Wegner 2014), dispersal in marine bryzoans (Burgess and Marshall 2011), and egg production in butterflies (Steigenga and Fischer 2007). Transgenerational plasticity may provide a more rapid response to novel environmental conditions than within-generational plasticity because maternal plants can provision their offspring in a way that minimizes the stress their offspring experience (Donohue and Schmitt 1998, Mousseau and Fox 1998, Dyer et al. 2010). In contrast, within-generational plasticity is inherently delayed as species sense a cue and respond appropriately, so offspring still experience stress (Weinig 2000, Chevin et al. 2010).

Both transgenerational plasticity and within-generational plasticity can affect the same trait such that the offspring phenotype depends on both the offspring environment and the environment their parents experienced. In plants, for example, germination often demonstrates both within- and transgenerational plasticity to temperature and light conditions experienced during maternal and offspring generations in species including *Plantago lanceolata* (Lacey 1996, Lacey and Herr 2000), *Leucanthemopsis alpina* (Bernareggi et al. 2016), *Brassica rapa* (Wadgymar et al. 2018) and *Arabidopsis thaliana* (Blödner et al. 2007, Donohue 2009, Whittle et al. 2009, Auge et al. 2017), and in *Campanula americana* seeds sown in light gaps had greater germination and survival than seeds sown in the shade, but only if their mother also grew in a light gap (Galloway and Etterson 2007). Although transgenerational plasticity can be maladaptive if environmental stress causes inferior offspring production or if parental and offspring environments are not well-matched (Stearns 1992, Marshall and Uller 2007, Munday et al. 2013, Munday 2014), adaptive transgenerational plasticity is predicted to evolve if the parental environment is predictive of the offspring environment (Kingsolver and Huey 1998, Herman et al. 2012, 2014, Burgess and Marshall 2014, Leimer and McNamara 2015, Colicchio and Herman 2020). Transgenerational plasticity, therefore, might promote rapid responses (and possible adaptation) to directional environmental change if parents can accurately convey information about novel conditions to their offspring (Donelson et al. 2018, Bell and Hellmann 2019).

Although phenotypic plasticity is a common response to global change, the extent of plastic responses often varies across species (Henn et al. 2018). A variety of life-history traits such as self-compatibility may affect the evolution of within- and transgenerational plasticity (Dury and Wade 2019), and several hypotheses speculate that phenotypic plasticity may facilitate biological invasions (Sultan 2001, Wolkovich and Cleland 2011), enabling them to colonize and establish in novel climates (Schlichting and Levin 1986). Indeed, nonnative species often demonstrate greater within-generational plasticity than native species (Richards et al. 2006, Davidson et al. 2011; but see Godoy et al. 2011). For example, nonnative species show greater increases in survival and growth than native species in response to nutrient addition and high light (Milberg et al. 1999, Gleason and Ares 2004, Leishman and Thomson 2005, Brock et al. 2005) and stronger advances in leaf-out and flowering time in response to warming (Crawley et al. 1996, DeFalco et al. 2007, Resasco et al. 2007, Xu et al. 2007, Godoy et al. 2009, Willis et al. 2010, Pearson et al. 2012, Wolkovich et al. 2013, Wilsey et al. 2015, 2018, Zettlemoyer et al. 2019). Such within-generational plasticity likely affects a species' establishment and spread, that is, its 'invasiveness' (van Kleunen and Richardson 2007), and could contribute to invasion success under global warming.

Similar to the explanations for greater within-generational plasticity in nonnative species, we hypothesize that nonnative species may also express greater transgenerational plasticity than native species for two reasons. First, transgenerational plasticity can more rapidly increase stress tolerance and fitness in offspring than within-generational plasticity. This could promote establishment of nonnative species in stressful habitats or result in more rapid population spread for widespread nonnatives (i.e. invasive species). For example, in nonnative *Cyperus esculentus*, maternal responses to nutrient-poor soil conditions promoted greater propagule dispersal in the next generation (Dyer et al. 2010). Second, nonnative species are more often self-compatible than native species (Baker 1955, Razanajatovo et al. 2016), and selfing makes transgenerational plasticity more likely to evolve (Dury and Wade 2019). Together, this suggests that nonnative species may be particularly likely to have greater transgenerational plasticity.

Here, we use seeds collected from a field warming experiment at the W.K. Kellogg Biological Station (KBS) to examine transgenerational and within-generation plasticity in response to warming in a suite of grassland species. Although we use the general term 'transgenerational plasticity', which includes non-genetic inheritance, parental effects, carry-over effects, intergenerational effects, seed provisioning, and epigenetic transmission (Donelson et al. 2018), we specifically test the effect of the maternal environment on offspring phenotypes, or maternal effects (Roach and Wulff 1987). We focus on early phenological and growth traits because both within- and transgenerational phenological plasticity (i.e. shifts in the timing of life-history events like germination and flowering) may be especially important responses for species success under climate change (Jump and Peñuelas 2005, Merilä and Hendry 2014, Bonamour et al. 2019) and because germination timing can be plastic and is linked to plant fitness (Kalisz 1986, Donohue 2002, Donohue et al. 2010, Cochrane et al. 2015, Leverett et al. 2018). Similarly, offspring growth often demonstrates transgenerational plasticity (Agrawal 2001, Galloway and Etterson 2007, Sultan et al. 2009, Latzel et al. 2010), potentially providing offspring an advantage in stressful conditions (Moles and Westoby 2006, Herman and Sultan 2011). Because nonnative species exhibit greater plasticity in flowering time than native species in this (Zettlemoyer et al. 2019) and other systems (Grman and Suding 2010, Wainwright and Cleland 2013, Balshor et al. 2017, Wilsey et al. 2018) and to test whether patterns of within- and transgenerational plasticity in germination and early growth are generalizable across native and nonnative species, we include multiple native and nonnative species in this study. This work extends studies investigating transgenerational plasticity in germination timing in response to temperature, which has largely been tested in single species, by examining whether transgenerational plasticity to warming is consistent across species and whether it differs between native and nonnative taxa. We ask: do germination and early growth demonstrate within- or transgenerational plasticity and if so, do native and nonnative species differ in their within- or transgenerational responses to warming temperatures?

Material and methods

To assess the roles of within- and transgenerational plasticity and their interaction on germination and early growth of grassland species in response to warming, we planted seeds from maternal plants that had been grown under an experimental warming simulation in the field into warmed and ambient growth chamber conditions in a full factorial design (maternal temperature environment × offspring temperature environment). Although each generation experienced different degrees of environmental control (i.e. maternal plants were grown in the field while offspring were grown in potting soil in a growth chamber), this design is common for testing maternal effects on germination (Galloway and Etterson 2007).

Maternal temperature environment

The simulated warming array in the field uses infrared heaters to elevate temperatures 3°C above ambient temperatures, matching regional predictions for climate warming in this area by the end of the 21st century (0.3–4.8°C) (Stocker et al. 2013). Warmed plots also have lower soil moisture (percent water content) than ambient plots (warming $\chi^2_{1,6} = 34.02$, p < 0.0001; ambient = 16.2% versus warmed = 9.31% water). The array has run over the growing season (April–October) since 2008. In spring 2012, we planted 52 species (25 native and 27 nonnative) into the old field community in each plot (n = 3 replicates/species/plot × 4 plots/warming treatment), although only 24 species (13 native and 11 nonnative) that successfully produced viable seeds in both warming treatments are used here. Study species were forb and grass species found in old fields or grasslands (Schultheis et al. 2015). We define native species as species naturally occurring in Michigan prior to European settlement and nonnative species as species introduced to Michigan from outside the United States. For a full description of the simulated warming experiment see Zettlemoyer et al. (2019). In this system, nonnative species exhibit advanced flowering phenology relative to native species and accelerate flowering in response to warming more so than native species, although prior studies did not investigate other phenological stages like germination timing (Zettlemoyer et al. 2019). However, because the study species are perennial, we focused on early growth stages and did not grow plants to flowering for this experiment.

To determine which plants produced viable seeds, we conducted germination trials using seeds from plants collected from the simulated warming experiment in the greenhouse (n = 41 species; 21 native and 20 nonnative) (greenhouse conditions were 29°C with a 16-h photoperiod). Seeds were collected from the field in 2013 and stored in a cool, dark cabinet until 2019. However, we did not account for variable dormancy requirements among species (e.g. stratification), potentially limiting germination and restricting our experiment to those species with lax germination requirements. We planted seeds in low-nutrient potting media and monitored daily seedling emergence over six weeks. Twenty-four species (13 native and 11 nonnative) successfully germinated in the greenhouse. We included all species with at least 20% germination in an attempt to boost the number of native species included in our study. For each of those 24 species, we selected seeds from 3 to 5 individuals grown under ambient field maternal conditions and another 3–5 individuals grown under warmed field maternal conditions. When possible, we elected to use seeds from maternal plants from different field plots. We ended up with 116 total maternal plants spanning the 24 species (3–5 individuals per maternal environment per species).

Offspring temperature environment

To set growth chamber/offspring temperature conditions, we collected daily maximum and minimum temperatures from 1

April to 30 June 2013 (approximately the time period when germination occurs in the field) from the CLIMOD database (<http://climod2.nrcc.cornell.edu/>). We used these day and night temperature extremes observed in the field dataset to program daily temperature curves for each growth chamber, with the warmed chamber set to be consistently 3°C warmer than the ambient chamber. Day length was set at 14 h, roughly matching photoperiod in the field. This design allows us to separate effects of maternal temperatures (i.e. temperatures experienced during seed maturation in the field) versus offspring temperatures (i.e. temperatures experienced post-dispersal in the growth chamber) (Burghardt et al. 2015).

We planted three seeds from each maternal plant into separate conetainers filled with low-nutrient potting media and placed them into ambient and warmed growth chambers (n = 3 replicates × 116 maternal plants × 2 chamber temperatures = 696 seedlings). We rotated trays between chambers every three days to minimize chamber effects and watered as needed to maintain similar moisture levels between treatments. Germination (indicated as cotyledon emergence) was recorded daily. We measured seedling height (the longest leaf; cm) at the end of the experiment.

Data analysis

To examine whether native and nonnative species' germination and early growth (seedling height) demonstrate within- or transgenerational plasticity in response to temperature, we used generalized linear mixed models fit in the lme4 package in R ver. 3.0.2 (Bates et al. 2015, <www.r-project.org>). We conducted three models with three separate response variables: 1) germination success (1 = yes, 0 = no; binomial distribution), 2) days to germination (negative binomial distribution for overdispersed count data; Lindén and Mäntyniemi 2011), excluding ungerminated seeds and 3) seedling height (cm; Gaussian distribution). For germination success, we included maternal temperature environment (E_M; ambient versus warmed field conditions), offspring temperature environment (E_O; ambient versus warmed chamber conditions), status (native versus nonnative) and their interactions as predictor variables. We included species (nested within status) and field plot (nested within maternal environment) as random effects. For days to germination and seedling height, we only included species that successfully germinated in all temperature combinations (n = 3 native and 5 nonnative species). Due to resulting low sample sizes, we could not test interactions between maternal and offspring environments. We instead ran two models for each response variable, one for 1) transgenerational plasticity and another for 2) within-generational plasticity. Models for 1) transgenerational plasticity included status, E_M and status × E_M as predictor variables and species (nested within status) and plot (nested within E_M) as random effects. Models for 2) within-generational plasticity were identical but included E_O instead of E_M. For seedling height models, because seedling height depends on germination time, we first regressed height against days

to germination for each species. We subsequently used the residuals as the response variable for the third model, thereby removing variation in height due to differences in germination phenology. We provide the results of models using height as a response variable in the Supporting information (results are qualitatively similar).

We used similar models to examine variation in within- and transgenerational plasticity in germination success, germination timing and seedling height among species regardless of status. For germination success, we included species, E_M, E_O and their interactions as predictor variables, with plot (nested in E_M) as a random effect. For days to germination and seedling height (residuals), we again only included the eight species that successfully germinated in all temperature combinations. Like above, we ran two models each for days to germination and seedling height, one for 1) transgenerational and another for 2) within-generational plasticity. These models, respectively, included 1) species, E_M and species × E_M and 2) species, E_O and species × E_O as predictor variables. We included field plot (nested in E_M) as a random effect in all models. Following significant interactions between species × E_M and species × E_O for days to germination and seedling height, we conducted individual species models. For species with sufficient sample sizes, we examined the effects of E_M, E_O and the interaction of E_M × E_O on days to germination and seedling height. For species with low sample sizes where E_M × E_O could not be estimated, we removed the interaction and only tested the main effects of maternal and offspring temperatures. Field plot (nested in E_M) was included as a random effect in all individual species models. Individual species models were not conducted for germination success because we detected no evidence for species-specific responses to temperature.

Finally, to investigate whether and how plasticity in germination timing is associated with plasticity in other phenological stages, we compared both within- and transgenerational plasticity in germination timing found here to within-generational plasticity in flowering time from Zettlemoyer et al. (2019) (again using only the eight species that germinated in every temperature combination). Within-generational phenological plasticity was calculated as the difference in mean offspring phenotype ($\bar{X}$; that is, germination timing or flowering time) when offspring experienced warmed versus ambient temperatures (Valladares et al. 2006):

Within-generational phenological plasticity

$$= X_{offspring.warmed} - X_{offspring.ambient}$$

Transgenerational phenological plasticity was calculated as the difference in mean offspring phenotype when maternal plants experienced warmed versus ambient temperatures:

Transgenerational phenological plasticity

$$= X_{maternal.warmed} - X_{maternal.ambient}$$

We used differences for phenological plasticity because proportional responses for phenological estimates would cause later flowering individuals to appear to be less plastic when they could in fact be advancing flowering time as much as early flowering individuals.

We calculated within- and transgenerational plasticity in early growth as the proportional difference in mean offspring phenotype (seedling height) when offspring or maternal plants (respectively) experienced warmed versus ambient temperatures:

Within-generational plasticity in early growth

$$= \frac{X_{\text{offspring.warmed}} - X_{\text{offspring.ambient}}}{X_{\text{offspring.ambient}}}, \text{ and}$$

Transgenerational plasticity in early growth

$$= \frac{X_{\text{maternal.warmed}} - X_{\text{maternal.ambient}}}{X_{\text{maternal.ambient}}}$$

We averaged responses to temperature within generations because we detected no interactions between maternal and offspring temperatures. We then estimated Pearson's correlations among within-generational plasticity in flowering time, within-generational plasticity in germination timing, transgenerational plasticity in germination timing, within-generational plasticity in early growth (seedling height), transgenerational plasticity in early growth and mean early growth.

Results

Nonnative species tended to be approximately twice as likely to germinate than native species (status $\chi^2_{1,0.005} = 3.30$, p = 0.06; Supporting information; Fig. 1). We detected no evidence that temperatures experienced by either maternal or offspring generations affected germination success in native or nonnative species or across species (all $E_M \times$ status {or species} and $E_O \times$ status {or species} interactions, p > 0.5, Supporting information).

Species varied in their germination timing responses to warming during maternal generations ($E_M \times$ species $\chi^2_{7,202} = 17.56$, p = 0.02; Supporting information). On average, warmer temperatures experienced during the maternal generation delayed germination by 0.20 ± 0.1 days °C^{-1} relative to ambient temperatures (E_M: $\chi^2_{1,5.86} = 3.58$, p = 0.05; Fig. 2a). Three native species, *Achillea millefolium*, *Panicum virgatum* and *Coreopsis lanceolata*, and two nonnative species, *Dactylis glomerata* and *Gaillardia pulchella*, demonstrated this pattern, with all other species not responding significantly to maternal temperature environments (E_M: AM $\chi^2_{1,13} = 3.09$, p = 0.07; CL $\chi^2_{1,3.24} = 5.91$, p = 0.01; PV $\chi^2_{1,5} = 4.09$, p = 0.04; DG $\chi^2_{1,16.81} = 4.65$, p = 0.03; GP $\chi^2_{1,3} = 5.66$, p = 0.02; Table 1, Fig. 2b).

In contrast, germination timing responses to offspring warming were much weaker and did not vary substantially across species (E_O: effect size = -0.11 ± -0.10 days °C^{-1} earlier under warmed relative to ambient temperatures; $\chi^2_{1,190.37} = 1.14$, p = 0.2; Supporting information; Fig. 2c; species $\times E_O$ $\chi^2_{7,202} = 7.31$, p = 0.4; Supporting information). Native *C. lanceolata* and nonnative *D. glomerata*, *Hypericum perfoliatum* and *Phleum pratense* germinated earlier under warmed relative to ambient offspring temperatures, but no other species responded significantly to offspring temperatures (EO: CL $\chi^2_{1,2.01} = 11.17$, p = 0.0008; DG $\chi^2_{1,47.74} = 2.15$, p = 0.1; HP $\chi^2_{1,18.27} = 4.15$, p = 0.04; PP $\chi^2_{1,44.73} = 2.44$, p = 0.1; Table 1, Fig. 2d). We detected no consistent differences in germination phenology between native versus nonnative species in response to temperatures experienced by either generation (Supporting information).

Warming during both maternal and offspring generations affected plant height, although the direction of effects varied across species (species $\times E_M$: $\chi^2_{7,184.68} = 32.82$, p < 0.0001;
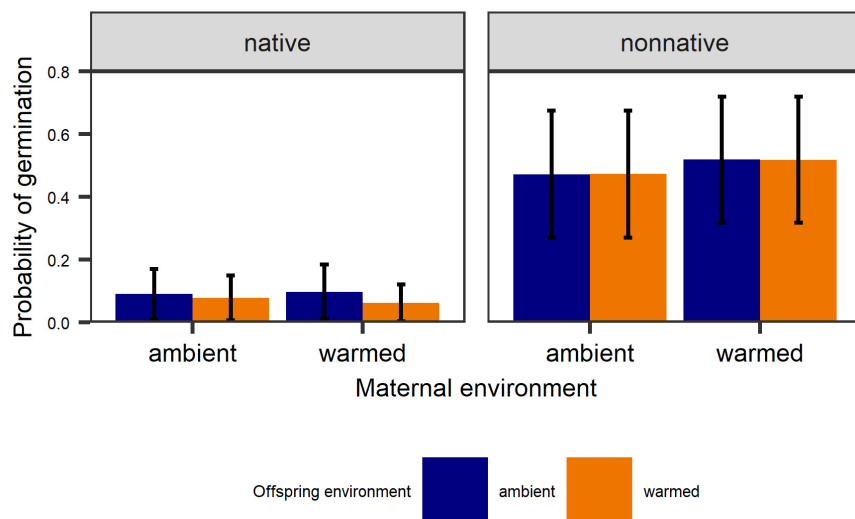

Figure 1. Germination success (proportion of seeds germinated; least square means ± standard error) under ambient versus warmed (+3°C) maternal environments (x-axis) and ambient (blue) versus warmed (orange) offspring environments in native (left) versus nonnative (right) species.
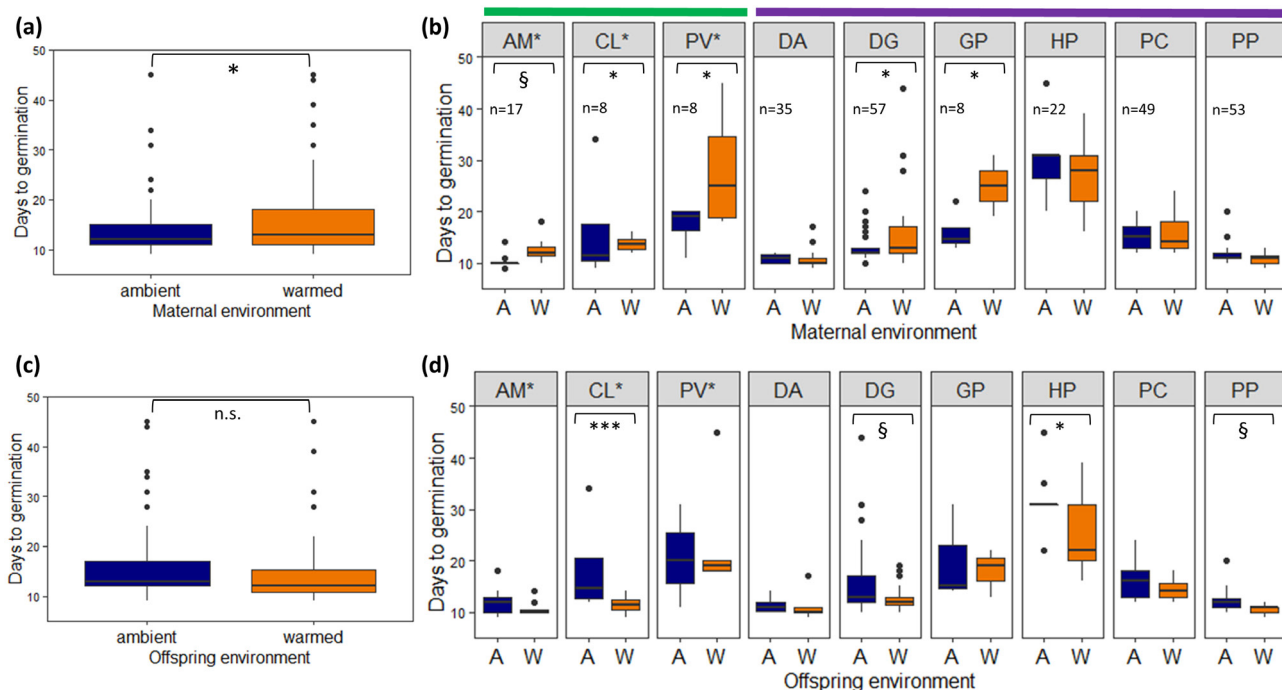
Figure 2. Days to germination under ambient (blue) versus warmed (+3°C; orange) (a) maternal environments or (c) offspring environments. (b) and (d) show species-specific response to maternal and offspring temperatures, respectively. Native species are indicated with asterisks and green lines, while nonnative species are indicated with purple lines. An asterisk within a bracket indicates that species differed in germination timing between ambient versus warmed temperatures (Tukey tests, $\alpha = 0.05$), where *** p < 0.0001, * p < 0.05, $\S$ p < 0.1. We provide sample sizes in the top species panels.

species $\times$ E_O: $\chi^2_{7,184.22} = 13.57$, p = 0.05; Supporting information; Fig. 3). On average, seedlings tended to grow more rapidly than expected under warmed relative to ambient offspring environments (E_O: $\chi^2_{1,192.93} = 3.23$, p = 0.07; Fig. 3c; Supporting

information), with three nonnative species, *D. glomerata*, *G. pulchella* and *Poa compressa*, growing significantly more rapidly under warmed offspring conditions (DG: $\chi^2_{1,53} = 6.41$, p = 0.01; GP $\chi^2_{1,3} = 6.35$, p = 0.01; PC $\chi^2_{1,41.09} = 5.55$, p = 0.02;

Table 1. Species-specific models for the effect of maternal and offspring temperatures on germination and early growth. Results of generalized linear mixed models (GLMMs) for individual species' germination success (1 = yes, 0 = no; binomial distribution), (B) germination timing (days to germination; negative binomial distribution) and (C) height (residuals after controlling for germination timing; Gaussian distribution). We included offspring environment (E_O; ambient versus warmed chamber conditions), maternal environment (E_M; ambient versus warmed field conditions) and their interaction as fixed predictor variables (where possible). Plot (nested in maternal environment) was included as a random effect in each model. '–' indicates that a parameter was not estimated due to low power. *** p ≤ 0.0001, ** p ≤ 0.01, * p ≤ 0.05, ·p ≤ 0.1. Bold indicates p ≤ 0.01.

| Species	Germination timing χ^2			Height (residuals) χ^2		
	E_O	E_M	$E_M \times E_O$	E_O	E_M	$E_M \times E_O$
Natives						
Arabis glabra (AG)	2×10^{-04}	3×10^{-04}	2×10^{-04}	0.00	3×10^{-04}	2×10^{-04}
Achillea millefolium (AM)	0.18	**3.09·**	1.44	0.00	0.00	0.25
Coreopsis lanceolata (CL)	**11.18*****	**5.91***	NA	**22.59*****	**78.66*****	NA
Penstemon hirsutus (PH)	–	–	–	–	–	–
Panicum virgatum (PV)	0.03	**4.09***	–	0.00	0.79	–
Nonnatives						
Bromus inermis (BI)	–	–	–	–	–	–
Leucanthemum vulgare (LV)	–	–	–	–	–	–
Centaurea maculosa (CM)	–	–	–	–	–	–
Dianthus armeria (DA)	0.62	0.06	0.21	0.09	0.29	1.02
Dactylis glomerata (DG)	0.28	**4.65***	2.15	**6.41***	1.08	0.03
Gaillardia pulchella (GP)	0.32	**5.66***	–	**6.35***	0.45	–
Hypericum perfoliatum (HP)	**4.15***	1.51	–	**7.29****	0.05	–
Melilotus officinalis (MO)	–	–	–	–	–	–
Poa compressa (PC)	0.25	0.03	0.11	**5.55***	0.19	0.01
Phleum pratense (PP)	**2.44·**	0.47	0.02	0.00	0.00	0.98
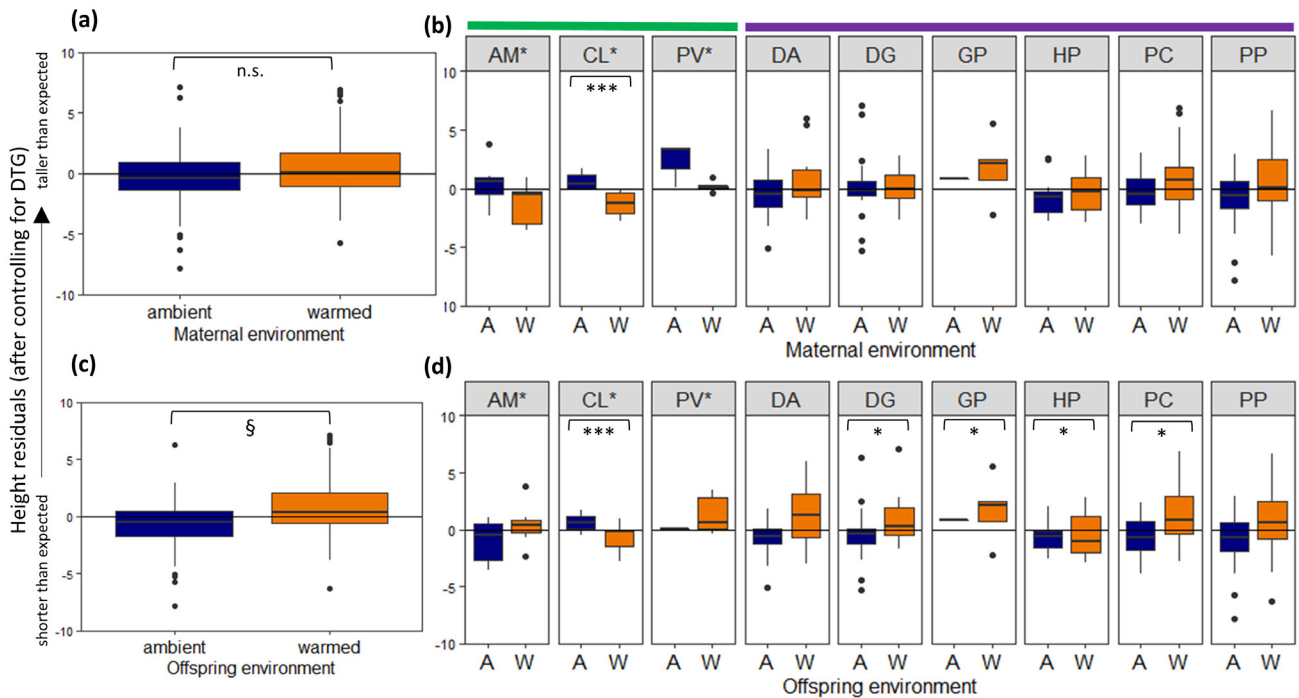
Figure 3. Residuals of seedling height (cm; after removing variation due to days to germination) under ambient (blue) versus warmed (+3°C; orange) temperatures experienced during (a) maternal or (c) offspring generations. (b) and (d) show species-specific response to maternal and offspring temperatures, respectively. Positive residual values indicate more rapid growth (i.e. taller seedlings) than expected based on germination timing. Native species are indicated with asterisks and green lines, while nonnative species are indicated with purple lines. An asterisk within a bracket indicates that species differed in early growth between ambient versus warmed temperatures (Tukey tests, $\alpha = 0.05$), where *** $p < 0.0001$, * $p < 0.05$, § $p < 0.1$.

Table 1, Fig. 3d). However, native *C. lanceolata* and nonnative *Hypericum perforatum* grew more slowly under warmed temperatures (CL $\chi^2_{1,2.10} = 22.59$, $p < 0.0001$; HP $\chi^2_{1,18.72} = 7.29$, $p = 0.007$). Seedling height responses to maternal temperature conditions were weaker, with only native *C. lanceolata* responding significantly to the maternal temperature environment. It grew more slowly than expected (i.e. seedlings were shorter than expected after controlling for differences in height due to variation in germination phenology) under ambient relative to warmed maternal environments ($\chi^2_{1,3.40} = 78.65$, $p < 0.0001$). As with germination timing, we detected no evidence that native and nonnative taxa differed in within- or transgenerational plasticity in height.

Correlations among plasticity in germination and flowering phenology

Within-generational plasticity in germination timing, transgenerational plasticity in germination timing, and plasticity in flowering time were not correlated (Supporting information), with one possible exception. Within-generational plasticity in germination timing was negatively correlated with within-generational plasticity in early growth ($r = -0.84$, $p = 0.006$; Supporting information), suggesting that species that are more plastic in their germination timing in response to temperatures experienced as offspring are less plastic in their growth rates.

Discussion

Effects of warming temperatures on germination phenology

Consistent with the few prior investigations of maternal warming, we found that warming experienced during the maternal generation, on average, delayed germination in the offspring generation. For example, warming during maternal generations results in delayed bud burst in *Populus nigra* (Dewan et al. 2018), and shorter winters as a result of warming temperatures can also delay offspring germination (Walck et al. 2011). Similarly, stressful or unfavorable conditions during maternal generations delay germination in species such as *Arabidopsis thaliana* (Donohue et al. 2005), *Pinus pinaster* (Cendán et al. 2013) and *Banksia* species (Cochrane et al. 2014) (but see Moriuchi et al. 2016, Walter et al. 2016). If warmed environments are similarly stressful, then delayed germination in response to warming temperatures experienced by maternal plants may reflect this stress response. Such responses could be adaptive and a strategy to avoid future stressful conditions (i.e. predictive plasticity or predictive germination) (Cohen 1967, Gremer et al. 2016), if delayed germination reduces the likelihood of experiencing conditions with catastrophic fitness effects (e.g. frost; Milbau et al. 2009). Delaying germination in stressful environments is also predicted to reduce

the risk of all seeds germinating into an unfavorable environment, thereby reducing temporal variation in fitness (Clauss and Venable 2000, Simons 2011, Gremer and Venable 2014, Gremer et al. 2016). However, these hypotheses require future work investigating whether delayed germination in response to warming parental environments corresponds with higher fitness under warming temperatures.

In contrast to our finding of delayed germination in response to maternal warming, warming during the offspring generation has minimal effects, but tended to act in the opposite direction by advancing germination phenology as might be expected given many species' temperature cues for germination. The three species responding significantly to warming during the offspring generation all responded by advancing germination. Other studies frequently detect advancing germination (Milbau et al. 2009, Zettlemoyer et al. 2017), leaf-out (Basler and Körner 2014, Geng et al. 2020) and flowering under warmer conditions (Fitter and Fitter 2002, Parmesan and Yohe 2003, Thackeray et al. 2016). Earlier germination can provide earlier access to resources like space, water and light via priority effects (Wolkovich and Cleland 2011, Wainwright et al. 2012), allows for earlier growth relative to other species in the community (Dickson et al. 2012, Fridley 2012, Wilsey et al. 2015), and can increase chances of surviving to reproduction (Leverett et al. 2018) and enhance plant fitness (Verdú and Traveset 2005). However, as climate change continues to alter local environmental conditions in a directional manner, mismatched responses between maternal and offspring generations, as detected here, could reduce plant fitness by counteracting one another and minimizing the phenological response.

Correlations among plasticity in germination and flowering phenology

Overall, our results suggest that plasticity in one life-history stage does not predict plasticity in another. If plasticity in germination timing and flowering time are truly not correlated, these traits could evolve separately in response to local environmental conditions as opposed to representing a correlated response to warming temperatures (Burgess et al. 2007). However, multiple species demonstrated consistent patterns in phenological plasticity across life-history stages; *Coreopsis lanceolata*, *Hypericum perforatum*, *Dactylis glomerata* and *Phleum pratense* all tended to advance flowering under warming (Zettlemoyer et al. 2019) and also tended to advance germination timing under warmed offspring environments. Some of these species also demonstrated transgenerational plasticity. For one species, *Panicum virgatum*, germination responses to maternal warming were in the same direction as flowering responses to warming temperatures (i.e. a tendency for delayed flowering and germination in response to warming in both generations), but for the other, *C. lanceolata*, the transgenerational response opposed both within-generational germination plasticity and flowering plasticity to warming (i.e. maternal warming delayed germination while offspring warming accelerated both germination and flowering).

Differences between native and nonnative species

In contrast to previous studies detecting earlier and more plastic germination phenology in nonnative species than natives in response to rising temperatures (Gerlach and Rice 2003, Seabloom et al. 2003, Resasco et al. 2007, Xu et al. 2007, Abraham et al. 2009, Grman and Suding 2010, Wainwright and Cleland 2013, Balshor et al. 2017, Wilsey et al. 2018; reviewed in Gioria and Pyšek 2017), we detected no differences in germination phenology between the native and nonnative species studied here in response to either maternal or offspring temperatures, although we had limited power (eight species) to detect such effects. Similar germination phenology between native and nonnative species has been observed in *Impatiens* species (Laube et al. 2015) and between native versus nonnative populations of *Hieracium pilosella* and *Hypericum perforatum* (Beckmann et al. 2011). Other species characteristics beyond native or invasive status are also predicted to influence the evolution of transgenerational plasticity. For example, theory predicts that self-incompatibility should correlate with lower transgenerational plasticity (Dury and Wade 2019). Counter to this prediction, all four species that demonstrated transgenerational plasticity in our study by delaying germination under maternal warming are self-incompatible (Supporting information). While a greater complement of species would be needed to rigorously test the association between mating system and transgenerational plasticity, it is possible that the transgenerational plasticity observed here is a maladaptive stress response, rather than the adaptive transgenerational plasticity modeled in Dury and Wade (2019).

Similar to the germination timing results, we also detected no evidence that nonnative species exhibited more plastic growth responses to warming. However, three of the six nonnative species studied here (*Dactylis glomerata*, *Gaillardia pulchella* and *Poa compressa*) demonstrated within-generational plasticity to warming temperatures via greater early growth. While this result in part supports previous findings suggesting that invasive species' growth and fitness increase under warming conditions (Parker-Allie et al. 2009, Verlinden and Nijs 2010, Compagnoni and Adler 2014), potentially providing invasive species with an advantage under climate change (Hellmann et al. 2008), it also suggests that these growth benefits are not pervasive and that warming may lead to increased success of some, but certainly not all, invasives.

Nonnative species had a higher probability of germination than native species regardless of temperature, consistent with other studies comparing germination success in native versus nonnative species (Colautti et al. 2006, Beckmann et al. 2011, Wainwright and Cleland 2013, Balshor et al. 2017). On one hand, this could be due to harvesting time: native species flower later in this system, and some of the latest flowering species (e.g. *Aster pilosis* and *Solidago canadensis*) likely had less-ripe seeds at collection. We checked for seed viability using tetrazolium assays; similar percentages of seeds were viable in native versus nonnative species (although nonnative species tended to have more viable seeds; Supporting information; status $\chi^2_{1,34} = 2.25$, p = 0.14), suggesting that differences in

seed viability did not influence our results. Alternatively, this could be due to higher thresholds for breaking dormancy in native species, wherein seeds require a cold period (i.e. vernalization) and an environmental cue that conditions are suitable for germination and growth (Fenner and Thompson 2005, Baskin and Baskin 2014). Future studies should account for species differences in requirements to break dormancy (e.g. stratification, diurnal versus nocturnal temperatures, photoperiod). We did not include a stratification treatment in this study, which could limit germination success (Munir et al. 2001). However, as temperatures warm, native species may be less likely to experience sufficient vernalization (Murray et al. 1989, Schwartz and Hanes 2010, Cook et al. 2012, Fu et al. 2015). Additionally, nonnative species may have broader germination requirements than native species (Gioria and Pyšek 2017), so future work should test whether the invasive species have similarly high germination success in field conditions. Ultimately, higher germination success in nonnative species suggests that germination could increase nonnative species' population growth rates relative to native species because germination plays an important role in determining population growth rates (Picó 2012, Leverett et al. 2018).

Conclusions

We find that maternal warming delays germination and that warmed temperatures experienced during the offspring generation tend to advance germination, although this latter pattern is weaker and not statistically significant. Our results indicate that temperatures experienced by maternal plants can impact their offspring's germination phenology, potentially even more so than temperatures experienced by the offspring themselves. This study furthers our understanding of both within- and transgenerational plasticity to temperature during early life-history stages, but future work is needed to understand the potential benefits or consequences of delayed germination under maternal warming.

Author contributions

Meredith A. Zettlemoyer: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (lead); Supervision (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jennifer A. Lau**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Resources (lead); Writing – review and editing (supporting).

Data accessibility

Upon publication, all data for this study will be available as .csv files in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.n2z34tmx9> (Zettlemoyer and Lau 2021).

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