MATERNAL ENVIRONMENT INFLUENCES PROPAGULE PRESSURE OF AN INVASIVE PLANT, *RAPHANUS RAPHANISTRUM* (BRASSICACEAE)

Lesley G. Campbell,[1],* Rebecca J. Parker,* Graham Blakelock,[2],* Natalia Pirimova,* and Kristin L. Mercer†

*Department of Chemistry and Biology, Ryerson University, Toronto, Ontario M5B 2K3, Canada; and †Department of Horticulture and Crop Science, Ohio State University, Columbus, Ohio 43210, USA

Editor: Michele R. Dudash

Premise of research.   Weedy species that invade new areas may experience shifts in environmental conditions across generations. Since maternal environments can significantly influence embryo development, shifts in maternal environments could alter the ability of offspring to colonize.

Methodology.   Here, we report the results of a set of field experiments that study adaptive transgenerational plasticity across three generations using the agricultural, annual weed, *Raphanus raphanistrum*. We grew replicate lineages across a gradient of experimentally manipulated soil moisture conditions (control rain [×2], no rain, double normal precipitation) for two generations (maternal and offspring) and transplanted individuals of each population to manipulated or unmanipulated soil moisture conditions. We then measured the consequences of the maternal and offspring soil moisture manipulations on traits critical for weediness in the second generation of plants and third (grandchild) generation of seeds.

Pivotal results.   Maternal moisture environments significantly influenced offspring development. Offspring of parents from relatively dry environments were significantly smaller (reduced seed biomass, floral displays, and size at reproduction) and less fecund, while offspring of parents from relatively wet environments were significantly larger and more fecund compared with related offspring whose parents had been grown under control moisture conditions. The relative differences among lines grown under various maternal environments were intensified when they were grown in a common environment.

Conclusions.   Weediness is a product of the population genetics of colonists and environmental characteristics of the invaded environment. Plastic responses to abiotic variation experienced by the maternal parent or offspring may also influence the outcome of dispersal, potentially increasing the relative rate of movement or propagule pressure from relatively wet maternal habitats to dry recipient habitats. Possible implications of these environmentally induced phenotypes are discussed with respect to ecological distribution, persistence under novel environments, and evolution in natural populations.

Keywords: common garden, experimental evolution, fecundity, intergenerational plasticity, maternal effects, Ontario, Canada.

Online enhancements: appendix tables.

Introduction

Invasive plants cause harm to native ecosystems by competing for space and resources (Levine et al. 2003), altering landscape-level processes (Brooks et al. 2004; Dukes and Mooney 2004; Norkko et al. 2012), and compromising native genomes via hybridization with neighbors (Rhymer and Simberloff 1996; Burgess et al. 2005). There are several competing hypotheses surrounding the evolution of invasiveness (Theoharides and Dukes 2007; Whitney and Gabler 2008).

Plants may initially arrive at a new location because of their dispersal traits (Baker and Stebbins 1965; Rejmánek and Richardson 1996) or the movement patterns of their vectors (Vermeij 2005; Pauchard and Shea 2006). Plants may be able to colonize new locations when they possess adaptive weedy traits (Goodwin et al. 1999), when they arrive in a suitable habitat (Mack 1995; Gallien et al. 2010), or when they can express different phenotypes in response to new environments, that is, when they express phenotypic plasticity (Richards et al. 2006). Transgenerational phenotypic plasticity can produce progeny predisposed to succeed in new locations with different environmental conditions. For instance, maternal response to environmental conditions can bestow traits on offspring that increase offspring fitness in these new and potentially stressful conditions (Dyer et al. 2010). Here, we show that the establishment of weedy populations of wild radish (*Raphanus raphan-*

istrum) may be influenced not only by their current environment but also by the maternal environment.

Rare cases exist of successful invasions when species move between distinct climates (e.g., *Conyza canadensis*; Mack 1995). More commonly, subtle environmental differences between source and recipient environments may promote or dampen invasion or spread via their influence on offspring performance in the early generations after arrival (Dyer et al. 2010). Environmental differences among prior and current maternal environments may, for example, alter offspring provisioning, confer greater stress tolerance, or have no effect at all (Widmer et al. 2007; Monty et al. 2009; Dyer et al. 2010; Skalova et al. 2011). We can better predict the potential impacts of climatic shifts on the success of invasive species by exploring the effect of abiotic factors on seed development and offspring fitness when plants have invaded a novel environment (Meineri et al. 2013).

Characteristics of the maternal environment (e.g., light, temperature, water, nutrients, and disturbance) can dramatically alter the resources available at reproduction and therefore the provisioning of resources to and development of offspring on maternal plants (Riginos et al. 2007; Galloway and Etterson 2009; Diggle et al. 2010). For instance, lettuce grown under cool conditions produced few, large seeds, whereas lettuce grown under warm conditions produced many, smaller seeds (Drew and Brocklehurst 1990). Facilitated by hormones and enzymes involved in ovule and zygote development, resource allocation during seed development can affect offspring fitness, especially during the early life stages (Donohue and Schmitt 1998; Latzel et al. 2010; Li et al. 2011). Maternal effects can be weak relative to the direct effects of the offspring environment (Monty et al. 2009), yet the relative importance of maternal environment effects and offspring environment effects can change across conditions and increase the likelihood of invasion under certain conditions (Lacey and Herr 2000; Zhang et al. 2012).

The abiotic environmental characteristics that typify climate change such as increases in ambient CO_2 levels, elevated air temperatures, and altered rainfall patterns are known to affect plant fitness (Hedhly et al. 2009). These same environmental factors may also influence seed characters sensitive to changes in maternal environment, thereby altering offspring fitness (Zhang et al. 2012). Even small changes in maternal environments such as those associated with climate change or geographic migration between invaded sites can affect seed germination rates (Hoyle et al. 2013), seed germination phenology (Ctvrtlikova et al. 2012), seedling survival (Drescher and Thomas 2013), and plant growth (Bezemer and Jones 2012). Given that early life-history stages are most affected by maternal environments and early life stages are often critical to invasion success (Donohue 2009), it is important to understand the transgenerational effects of environmental variation on plant invasions.

Although many climate change studies have assessed how altering water availability directly affects seed germination and seedling growth (e.g., Hoyle et al. 2013; Kim and Donohue 2013), few climate change studies conducted in the field have considered indirect moisture effects from the maternal generation on the offspring generation (but see Gimeno et al. 2009; Beaton and Dudley 2010). Beaton and Dudley (2010) found that when grown under dry conditions, plants whose mothers had been grown in dry habitats did not possess physiological drought tolerance traits per se, yet they were larger as adults than plants whose mothers had been grown in wetter habitats. Further, fitness differences among *Quercus ilex* seedlings collected from populations with differing abiotic environments were largely due to maternal effects mediated by seed size and less due to physiological drought responses (Gimeno et al. 2009). Here, we examine how variation in soil moisture experienced by the maternal and offspring generations affects seed size, seedling growth, and reproductive success of a common agricultural weed, *R. raphanistrum* L. (wild radish or jointed charlock, Brassicaceae).

We test the hypothesis that maternal environmental conditions can facilitate invasion into a novel environment by testing predictions related to the performance of wild radish offspring invading environments more similar to versus more different from that of their maternal parent. This work contributes to the growing literature describing the relative importance of differences between the successfully and unsuccessfully invaded environments and the relationship of these differences to successful establishment of invading populations (Sakai et al. 2001; Dietz and Edwards 2006; Dyer et al. 2010). To that end, we asked the following questions: (1) How does the maternal environment affect seed biomass? (2) How do the maternal and offspring environments affect offspring fecundity? (3) How do life-history traits respond to transgenerational environmental differences? We discuss the potential implications of these processes for the invasion of weed populations into new locations as well as the evolution of weeds under conditions of climate change.

Methods

Study System

The self-incompatible *Raphanus raphanistrum* L. (wild radish or jointed charlock) is a widespread weed of Eurasian origin that grows in diverse soil moisture environments such as agricultural fields, disturbed areas, and coastal beaches (Holm et al. 1997; Warwick and Francis 2005). With its long-lived seed bank, early emergence after tilling, and annual growth habit, *R. raphanistrum* is a difficult weed to manage, especially in cereal crops (Warwick and Francis 2005). It grows a rosette with a thin, fibrous taproot. Reproductive success of this species largely depends on flowering time and rosette size (Campbell et al. 2009). Seedlings germinate in spring in disturbed ground, quickly followed by rosette development and flowering, with seeds produced between midsummer and the first frost (Warwick and Francis 2005).

From previous research, we have found that the fecundity of wild radish varies across environments (Campbell et al. 2006; Hovick et al. 2012), and we predicted that this may, in part, be a response to soil moisture. Although plant growth in *Raphanus sativus* (cultivated radish) can be largely determined by a combination of soil pH, phosphorus, and light availability, soil moisture also has a significant positive effect on biomass (Axmanova et al. 2011). Given their close taxonomic relationship, we expected a similar response from *R. raphanistrum*.

Seed Source and Study Sites

The seeds used in this experiment were originally collected from 60 plants across three natural *R. raphanistrum* populations in Binghamton, New York (Conner and Via 1993), where only yellow flower color was observed. The seeds were then subsequently grown in a common greenhouse environment for several generations, with population size increasing from 60 to >200 plants, in East Lansing, Michigan (Conner and Via 1993). We used seed from this population to establish our maternal generation (F_0). The maternal generation experiment was established at Waterman Farm, Columbus, Ohio (lat. 40°80′N, long. 83°01′W; elevation 306 m), in 2010. This site has a temperate climate; the total accumulation of precipitation in 2010 was 921 mm, and the July mean temperature that year was 25.0°C (van Oldenborgh and Burgers 2005).
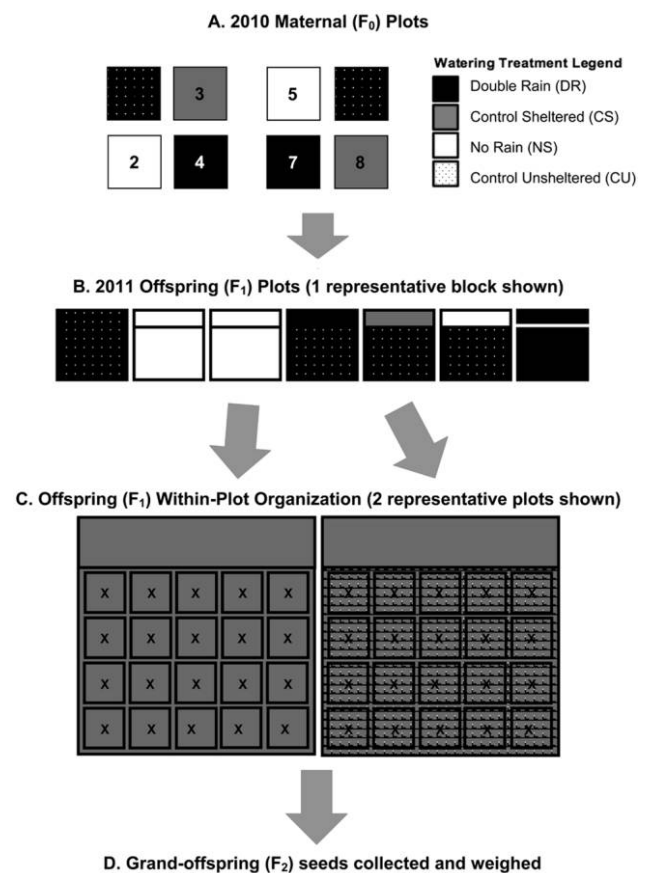
Field sites moved from Ohio to Ontario when the Campbell Lab relocated to Ryerson University, Toronto, Ontario. The offspring generation (F_1) experiment was performed in an old field located in King City, Ontario, at the Koffler Scientific Reserve on Jokers Hill (lat. 44°01′N, long. 79°32′W; elevation 285 m) in the Oak Ridges Moraine in 2011. This field site also experiences a temperate climate, with a total precipitation accumulation of 831.3 mm and a July mean temperature of 24.4°C (Environment Canada 2011). Thus, it was similar to the maternal environment in a number of respects. However, it may have also differed in some ways (e.g., nutrient levels or soil microbial community), so it likely presented some novel but unmeasured conditions.

Maternal Generation (F_0) Experiment

To measure the traits of two generations of *R. raphanistrum* with experimentally altered soil moisture, F_0 seeds were planted into one of four maternal environments with altered soil moisture (fig. 1A). A subsequent generation was planted into a second experiment, the offspring generation (F_1) experiment, detailed below and in figure 1B, 1C.

For this first generation, seeds from more than 200 F_0 maternal plants were germinated and grown to the two-leaf stage under greenhouse conditions in May 2010 at Ohio State University in Columbus. Then, in each of nine blocks, nine *R. raphanistrum* seedlings were transplanted into each moisture treatment plot, arranged in three rows of three with ~30-cm spacing. The treatment plots were assigned in a randomized complete block design. All of the 36 plots were at least 61 m from each other and scattered across Waterman Farm. In each plot, nine *R. sativus*, nine *Helianthus annuus*, and nine *Helianthus petiolaris* each occupied one-quarter of the plot because these species were being used to test hypotheses surrounding water availability and hybridization rates (Sneck 2013). Only nonhybrid *R. raphanistrum* F_1 offspring produced by the F_0 *R. raphanistrum* plants were used in this study. We did not receive permission to import the offspring of *R. sativus*, *H. annuus*, or *H. petiolaris* to Canada, and therefore these three species were not planted in the F_1 offspring plots. Each plot was tilled prior to transplanting, and competing weed populations were kept to a minimum for the remainder of the field season.

For the first week after transplanting, seedlings in all moisture treatments received equal amounts of supplementary wa-

A. 2010 Maternal (F_0) Plots

Watering Treatment Legend
Double Rain (DR)
Control Sheltered (CS)
No Rain (NS)
Control Unsheltered (CU)

B. 2011 Offspring (F_1) Plots (1 representative block shown)

C. Offspring (F_1) Within-Plot Organization (2 representative plots shown)

D. Grand-offspring (F_2) seeds collected and weighed

Fig. 1 Schematic of experiments to quantify effect of maternal soil moisture environment on phenotype of offspring and grandoffspring. *A*, For the maternal generation (F_0) experiment plots performed in Columbus, Ohio, we present a simplified representation of two of nine blocks from the randomized complete block design. The four plots per block were each randomly assigned one of the four experimental watering treatments, and nine F_0 seedlings were planted in each plot. While plots and blocks in *A* are represented in rows for schematic purposes, blocks and plots within blocks were scattered across the landscape with at least 61 m between each plot. *B*, *C*, In the offspring generation (F_1) experiment performed in King City, Ontario, 20 offspring (F_1) were planted into each plot (at each × denoted in *C*) in a partially reciprocal, randomized complete block design (with five blocks). Plots either received the maternal moisture treatment (from *A*) or were grown in control unsheltered conditions (for a total of eight treatment combinations and 800 plants in all). The smaller rectangle represents the maternal watering treatment, whereas the larger rectangle represents the offspring watering treatment. *D*, Five grandoffspring seeds (F_2) per F_1 plant grown in *B* and *C* were extracted from fruits and weighed (600 seeds total). All data except F_0 soil moisture and seed biomass and F_2 seed biomass were taken on F_1 plants.

ter. Once plants had established, experimental watering treatments were implemented for the remainder of the experiment. In order to control the amount of water applied to each plot, rain-exclusion shelters were built as described by Yahdjian and Sala (2002) with dimensions 3 m × 3.7 m. The rain-exclusion shelter roofs of translucent corrugated plastic (Waldo, Toledo, OH) were hung on an angle at least 1.2 m above the ground and drained the rain through eaves troughs into 227-L rain

barrels for collection. Watering treatments were applied to the F_0 generation as follows.

Control unsheltered (CU) treatment. There was no experimental manipulation of rainfall.

No rain (NR) treatment. We intercepted all rainfall with a rain-exclusion shelter (although rain blew in from the side of the structure). Therefore, no rain plots received very little rainfall.

Control sheltered (CS) treatment. As with the no rain treatment, we intercepted all rain and collected the water. However, collected rainwater was then applied to the plot within 48 h of the rain event. Therefore, control sheltered plots received any rain that would have otherwise fallen on the plots. This treatment serves as an appropriate control for the no rain and double rain plots as well as a useful experimental comparison with the control unsheltered plots.

Double rain (DR) treatment. As with the control sheltered treatment, we intercepted all rain and collected the water, which was then applied to the plot within 48 h of the rain event. In addition, the rainwater collected at the no rain plots was also applied to the double rain plots; therefore, double rain plots received twice the amount of rain that fell.

With high insect visitation to flowers, we noticed that maternal generation (F_0) plants produced abundant seeds in all plots. Although *R. sativus* was present within these maternal plots and is able to hybridize with *R. raphanistrum*, the actual hybridization rate was very low (<5%; L. G. Campbell et al., unpublished manuscript), and all hybrid offspring (9 of 800 plants), which are readily identifiable in the offspring generation (F_1) by their white flowers, were excluded from the experiment. We collected up to 18 fruits from the four central, maternal generation (F_0) plants per plot during three collection periods spread across the flowering season to generate up to 72 half-sib families per maternal plot. We did not control for paternal environmental effects. The five border plants were not sampled because they may have received more rain and because their relaxed and variable competitive environments may have altered maternal moisture environments for the seeds produced on the plants.

Offspring Generation (F_1) Experiment

The control unsheltered treatment represented a new offspring moisture environment relative to the maternal environment experienced by the control sheltered, no rain, and double rain maternal generation (F_0) plants. Thus, we considered the relative success of F_1 offspring plants growing in this novel environment to be indicative of their response to a newly colonized location. We contrasted this response to the relative change experienced for seeds planted into an environment more similar to that of their maternal environment (e.g., from maternal generation [F_0] control unsheltered to offspring generation [F_1] control unsheltered or from maternal generation [F_0] no rain to offspring generation [F_1] no rain).

To plant the offspring generation (F_1) experiment, we used the offspring from 12 randomly chosen maternal environment plots—three replicate plots from each treatment. The weighed seeds produced by F_0 plants were grown into seedlings and then planted into the offspring garden F_1 plots. We planted

the weighed seeds between June 1 and 3, 2011, in 25 mL of soilless medium (Promix BX; Premier Horticulture, Rivière-du-Loup, Quebec) in germination trays. Seedlings were grown to the two-leaf stage under greenhouse conditions in King Township, Ontario, and were each given 0.1 g of C-I-L blood meal (12-0-0; Canadian Tire, Newmarket, Ontario). One to three seedlings from each half-sib family were randomly allocated to replicate plots within the moisture environment experienced by their maternal parent or to replicate control unsheltered moisture environment plots. While we kept track of half-sib families for the purpose of planting plots and replicates with similar genetic compositions and levels of diversity, they were not part of our subsequent analyses, because full models with families included would not resolve due to limited degrees of freedom. However, informal analyses indicated variation among families for these responses, so future studies could be designed to target this level of analysis.

We tilled each plot three times during the week of June 20–24, 2011, transplanted the seedlings between June 27 and 30, and then erected rain-exclusion plots (July 4–6) for control sheltered, double rain, or no rain plots. Upon transplanting, each seedling received 1 L of water to ensure high survival. In 2011, whenever the area received rainfall, we applied the equivalent amount of local well water (not rainwater) to control sheltered plots and double the amount that had fallen as rain in double rain plots. In each of the 40 offspring generation (F_1) experiment plots, we planted four rows of five plants with 20 cm between plants (fig. 1*C*). Each plot was surrounded by two buffer rows of *R. raphanistrum*, and plots were weeded to ensure consistent levels of competition. Plants were sprayed once with Ortho Malathion on June 21 to reduce flea beetle herbivory (0.4% application rate; Scotts Miracle-Gro, Marysville, OH). A plant was harvested once it stopped producing flowers and at least 10 fruits were senescent and ready to dehisce.

Data Collection

In 2010, soil moisture was measured using a FieldScout time-domain reflectometer (TDR) 100/200 (Spectrum, Plainfield, IL) at the center of each plot approximately 24 h after bouts of natural rainfall (July 27 and 29; August 3, 7, and 11; September 2, 25, and 29; rainfalls after which soil moisture was not sampled include August 16 and 23). For the first sampling period, a single soil moisture reading was taken from the center of each plot. For every subsequent sampling period, average soil moisture per plot was calculated from three separate readings taken from haphazardly chosen central locations within each plot. In 2011, soil volumetric moisture content (VMC) was measured from three separate TDR readings taken from the center region of each plot subsequent to natural rainfall events and approximately 24 h after watering treatments were applied (July 20 and 26; August 5, 13, 18, and 23). We calculated average soil moisture per plot for each sampling period and overall, across sampling periods.

Our analysis focuses on phenotypic and fitness responses of the offspring generation (F_1), so all data on plant traits except F_0 and F_2 seed biomass were collected on that generation. Given that maternal environment may be reflected early in plant life

cycles, we recorded mass of seeds produced by a subset of maternal F_0 plants (four of nine in each plot). We weighed five seeds per fruit to a maximum of 90 F_1 seeds per maternal plant (i.e., seeds from up to 18 fruits).

For each offspring F_1 plant, we recorded age at first flower, stem diameter at first flower, flower number, fruit number, number of seeds per fruit, and biomass of five seeds per plant. Survival after transplanting was nearly 100% and will not be considered further. To measure fruit set, we counted number of fruits per plant. To estimate the number of seeds per plant, a value we assume is correlated with propagule pressure, we multiplied the average number of seeds per fruit (for 10 randomly chosen fruits per plant) by the number of fruits.

Statistical Analysis

All analyses were performed using SPSS v.13 (Chicago, IL) or SYSTAT v.11.00.01 (Richmond, VA), and block was treated as a random effect in the ANOVA. Throughout all analyses, variables were transformed as noted when they violated assumptions of normality of the residuals. Offspring F_1 individuals grown in the same plot lack statistical independence; therefore, trait values were averaged across plants grown within the same maternal plot. We used a post hoc Tukey HSD test to perform pairwise comparisons of treatments where we found significant effects.

Effects of watering treatments on soil moisture. First, we assessed whether the 2010 and 2011 watering treatments altered soil moisture. We used a repeated-measures mixed general linear model with an autoregressive covariance matrix that included watering treatment (between-subjects factor), date of moisture measurement (within-subjects factor), and their interaction (between-subjects by within-subjects interaction) as fixed effects (table A1, fig. 2; tables A1–A3 available online).

Transgenerational effects of the watering treatments. Second, to determine whether there were immediate and transgenerational effects of the moisture treatments, we performed three analyses. The analyses all used the same underlying model but used different subsets of the data to answer different questions. Each used a mixed-model ANOVA where block and F_0 plot were random effects and maternal watering treatment was a fixed effect.

a) Maternal effects on seed biomass, fecundity, and life history. To estimate maternal effects, we explored how the maternal environment affected seed biomass, fecundity (i.e., seeds per fruit, fruit per plant, seeds per plant), and life history of offspring grown in a novel environment (control unsheltered; table A2). The response variables included $\log_e$ days to flowering, stem diameter, $\log_e$ number of fruits per plant, seeds per fruit, and $\log_e$ total number of seeds per plant. To examine the immediate effects of the maternal generation experiment on F_1 seed biomass, we used a repeated-measures mixed-model ANOVA with an autoregressive covariance matrix that included the maternal (F_0) watering treatment (between-subjects factor) and harvest timing (early, midway, or late in the season; within-subjects factor) and their interaction as fixed effects (table A3).

b) Within-generation phenotypic plasticity. To measure within-generation phenotypic plasticity, we explored how the offspring environment affected the fecundity and life history
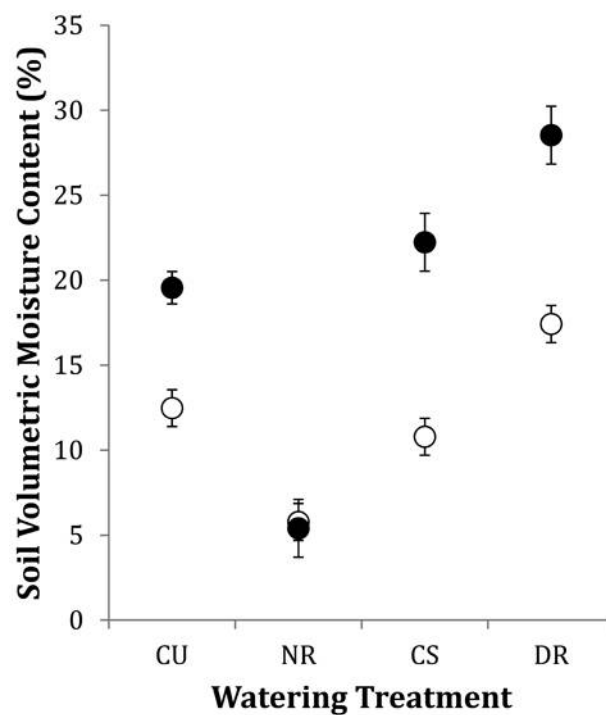
Fig. 2 Least squares mean volumetric moisture content ($\pm 95\%$ confidence interval) of soil in plots receiving one of four watering treatments (control sheltered [CS], control unsheltered [CU], double rain [DR], no rain [NR]) during the maternal generation (F_0) experiment in 2010 (open circles, back-transformed data) and offspring generation (F_1) experiment in 2011 (filled circles).

of offspring grown in identical maternal environments but under differing offspring watering treatment environmental conditions (table 1). We ran three ANOVAs, such that each ANOVA included the offspring of only one F_0 environment (e.g., double rain), allowing us to compare offspring phenotype grown under environmental conditions similar to (i.e., double rain) or different from (i.e., control unsheltered) the maternal environment in the F_1 generation. The response variables included days to flowering, stem diameter, number of fruits per plant, seeds per fruit, and total number of seeds per plant. To assess the transgenerational effects of the offspring generation experiment on the F_2 seed biomass, we used a linear mixed-model ANOVA, which included the offspring (F_1) watering treatment as a fixed effect. This was done two ways: we performed (i) three sub-analyses that held maternal F_0 environment constant and compared paired offspring treatments to understand the effect of the offspring environment (F_1) on F_1 traits and F_2 seed biomass (table 1) and (ii) a sub-analysis with data from only those plots that were grown under offspring (F_1) control unsheltered conditions to hold offspring generation environment constant while the maternal generation environment varied to understand the effect of the maternal environment (F_0) on F_2 seed biomass (table A2).

c) Cumulative environmental effects. Finally, to compare the degree of phenotypic differences of plants grown under the

Table 1

Effects of the Application of Maternal (F_0) or Control Unsheltered Watering Treatments on the *Raphanus raphanistrum* Offspring Phenotype (F_1) When Sharing a Common Maternal Environment

	NR		CS		DR	
	df	F	df	F	df	F
Log_{10} (days to flowering)	1, 22	.60	1, 21	.93	1, 22	.08
Stem diameter	1, 22	16.34***	1, 21	1.34	1, 22	10.11**
Log_{10} (fruit no.)	1, 22	9.98**	1, 21	13.10**	1, 21	6.91*
Seeds per fruit	1, 21	.06	1, 21	4.11[+]	1, 21	1.78
Log_{10} (total no. seeds)	1, 20	5.94*	1, 21	19.54***	1, 20	2.28
F_2 seed biomass	1, 24	15.01***	1, 24	.67	1, 24	.04

Note.   *F* statistics are given for moisture treatment, a fixed effect (offspring generation [F_1] environment). CS = control sheltered, DR = double rain, NR = no rain.

[+] $P < 0.10$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

four watering treatments, we analyzed the subset of plants where the offspring and maternal watering treatments were the same (table 2).

Results

Do Watering Treatments Alter Soil Moisture?

Experimental watering treatments significantly and predictably altered the average VMC in both years (fig. 2; table A1). No rain plots had significantly lower VMC than control sheltered plots, whereas double rain plots had significantly higher soil moisture. Finally, the VMC of control unsheltered and control sheltered plots did not differ significantly in 2010, whereas control unsheltered plots were slightly but significantly drier than control sheltered plots in 2011. Soil moisture declined significantly over the course of the growing season (table A1). Finally, there was a significant interaction between watering treatment and sampling date in both years (table A1), where the VMC of control sheltered and control unsheltered plots tended to decline significantly over the summer, whereas no

rain plots tended to remain relatively dry and double rain plots relatively wet.

Do Mothers in Resource-Rich Environments Better Provision Their Offspring Than Mothers in Resource-Poor Environments?

Maternal effects on seed biomass were apparent in both years; experimental watering of the maternal generation (F_0) significantly altered offspring (F_1) seed biomass (table A3). F_1 seeds produced in maternal generation (F_0) no rain plots weighed less than those produced in the maternal generation control unsheltered or control sheltered plots (fig. 3*A*). Similarly, experimental watering of the offspring generation (F_1) significantly altered grandoffspring seed biomass (tables 1, 2; fig. 3*B*). Further, F_2 seeds from plants grown under both maternal generation (F_0) and offspring generation (F_1) no rain plots were significantly lighter than F_2 seeds produced in all other plots (fig. 3*B*). Experimental watering in the F_0 maternal generation also had a significant effect on F_2 seed biomass (table A2); plants in control unsheltered conditions produced

Table 2

Effects of Soil Moisture Environments Consistently Applied for Two Generations (in Both the Maternal Generation [F_0] and Offspring Generation [F_1] Experiments) on the Fecundity of F_1 *Raphanus raphanistrum* from the Offspring Generation (F_1) Experiment

	ANOVA		Least mean squares (SE)			
	df	F	CU_{F_0}-CU_{F_1}	NR_{F_0}-NR_{F_1}	CS_{F_0}-CS_{F_1}	DR_{F_0}-DR_{F_1}
Log_e (days to flowering)	3, 44	.07	1.52 (.013)	1.51 (.013)	1.52 (.013)	1.52 (.013)
Stem diameter	3, 44	6.26***	6.02[AB] (.36)	5.74[AB] (.36)	5.11[A] (.36)	6.62[B] (.36)
Log_e (no. fruits)	3, 43	12.64***	2.39[BC] (.058)	2.14[A] (.058)	2.35[B] (.058)	2.54[C] (.059)
Average no. seeds per fruit	3, 42	.29	5.29 (.23)	5.07 (.24)	5.30 (.23)	5.38 (.24)
Log_e (no. seeds per plant)	3, 41	13.03***	3.12[BC] (.059)	2.88[A] (.060)	3.07[B] (.059)	3.28[C] (.060)

Note.   *F* statistics are given for the fixed-effect moisture treatment. CS = control sheltered, CU = control unsheltered, DR = double rain, NR = no rain. Subscripts indicate the generation to which the watering treatments were applied. Superscripts indicate statistical differences among least mean squares, when present.

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
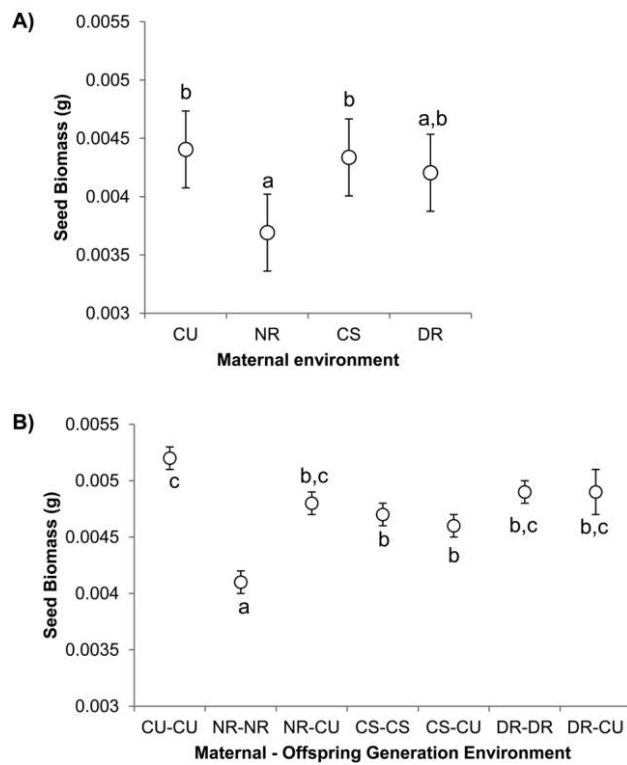
Fig. 3 Mean biomass ($\pm$ SE) of seeds produced during the maternal generation (F_0) experiment (*A*) and offspring generation (F_1) experiment (*B*) of *Raphanus raphanistrum* after plants received one of four watering treatments (control sheltered [CS], control unsheltered [CU], double rain [DR], no rain [NR]).

heavier grandoffspring than plants grown in control sheltered conditions (table A2; fig. 3*B*). Finally, harvest date of seeds had a significant effect on F_1 seed biomass (analysis in table A3), where seeds produced early in the season and midway through the season were significantly heavier than those produced late in the growing season (summarized data not shown).

How Does the Environment Affect Offspring Tendency to Be Invasive?

We found that offspring from mothers of resource-rich environments outperformed others when invading novel locations. Offspring (F_1) grown under control unsheltered environments whose mothers (F_0) were grown under double rain conditions were significantly more fecund than those offspring (F_1) whose mothers (F_0) were grown under the no rain or control sheltered conditions (table A2; fig. 4). Differences in fecundity were driven by significant differences in the number of fruits per plant ($F_{3, 43} = 3.41$, $P = 0.026$) and number of seeds per fruit ($F_{3, 42} = 3.62$, $P = 0.02$), where offspring (F_1) whose mothers (F_0) were grown under double rain conditions produced more fruit and more seeds per fruit than offspring (F_1) whose mothers (F_0) were grown under control sheltered conditions (tables A2, 3).

To assess the fitness consequences of offspring produced in a single maternal environment dispersing into a similar set of moisture conditions versus dispersing into a new (i.e., control

unsheltered) environment, we compared the fecundity of F_1 siblings raised in the control unsheltered plots and each manipulated moisture plot and found contrasting results. Offspring (F_1) grown under double rain conditions from mothers (F_0) grown under double rain conditions produced significantly more fruit (but not more seeds per plant) than siblings (F_1) grown under control unsheltered conditions from mothers (F_0) grown under double rain conditions (tables 1, 3; fig. 4); offspring (F_1) grown under no rain conditions from mothers (F_0) grown under no rain conditions produced fewer fruit and total seeds per plant than siblings (F_1) grown under control unsheltered conditions from mothers (F_0) grown under no rain conditions (tables 1, 3; fig. 4); offspring (F_1) grown under control sheltered conditions from mothers (F_0) grown under control sheltered conditions produced significantly more fruit and seeds per plant than siblings (F_1) grown under control unsheltered conditions from mothers (F_0) grown under control sheltered conditions (tables 1, 3; fig. 4).

Furthermore, we found that offspring produced in resource-rich environments outperformed plants produced in resource-poor environments when growing in their maternal environment. Offspring (F_1) grown under double rain conditions from mothers (F_0) grown under double rain conditions produced significantly more fruits and more seeds per plant relative to offspring (F_1) grown under control sheltered conditions from mothers (F_0) also grown under control sheltered conditions (tables 2, 3). Furthermore, offspring (F_1) grown under no rain conditions from mothers (F_0) also grown under no rain conditions produced fewer fruits and total seeds per plant relative
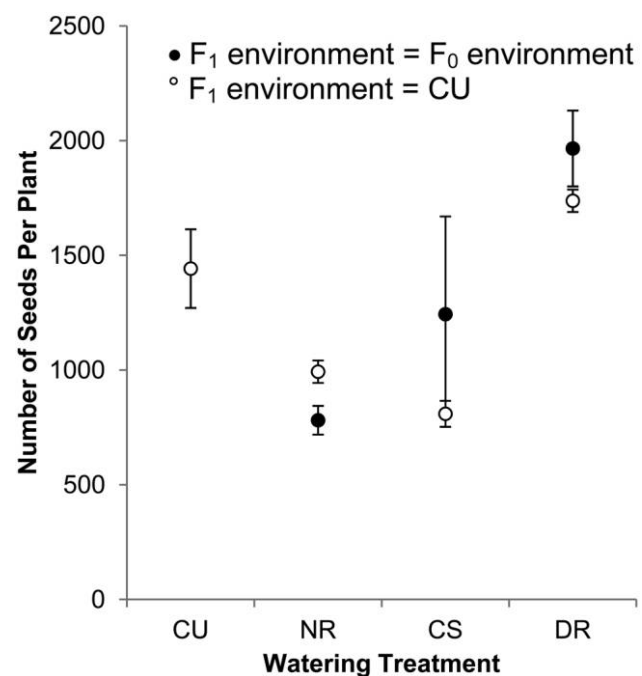
Fig. 4 Mean seed production ($\pm$ SE) in the offspring generation (F_1) experiment for offspring grown in their maternal environment and those that were moved to the control unsheltered (CU) environment. Maternal environment for *Raphanus raphanistrum* plants included CU, control sheltered (CS), double rain (DR), and no rain (NR).

Table 3

Summary Statistics of Several Key Life History Traits and Fitness Components from *Raphanus raphanistrum* Plants Grown in the Offspring Generation (F_1) Experiment (2011) in King City, Ontario

Maternal generation (F_0) treatment	Offspring generation (F_1) treatment	Age at flowering (d)	Stem diameter (mm)	Average no. seeds per fruit	No. fruits	No. seeds
CU	CU	33.25 (.53)	6.02 (.24)	5.27 (.14)	265.20 (28.00)	1442.30 (171.51)
CS	CS	33.10 (.32)	5.11 (.31)	5.30 (.16)	233.12 (19.86)	1243.60 (109.98)
CS	CU	33.48 (.46)	4.71 (.23)	4.91 (.17)	164.68 (12.99)	809.40 (56.63)
NR	NR	32.64 (.45)	5.74 (.19)	5.08 (.15)	145.85 (12.12)	781.35 (62.56)
NR	CU	33.06 (.49)	5.12 (.20)	5.03 (.17)	193.71 (16.81)	993.02 (98.59)
DR	DR	32.89 (.77)	6.62 (.22)	5.38 (.17)	360.89 (31.93)	1966.10 (165.24)
DR	CU	33.00 (.53)	5.88 (.18)	5.67 (.18)	280.43 (25.00)	1737.90 (172.38)

Note. Plants had been grown under four moisture treatments for two generations. CS = control sheltered, CU = control unsheltered, DR = double rain, NR = no rain. Mean values (SE) are presented.

to offspring (F_1) grown under control sheltered conditions from mothers (F_0) also grown under control sheltered conditions (tables 2, 3).

How Do Life History Traits Respond to Generational Differences in Environment?

Stem diameter demonstrated within-generational (table 1) and transgenerational (table A2) plasticity in response to moisture variation, whereas flowering time was insensitive to moisture variation (tables 1, A2). Offspring (F_1) grown under control unsheltered conditions whose mothers (F_0) were grown under either control unsheltered or double rain conditions grew significantly larger stem diameters than offspring (F_1) grown under control unsheltered conditions whose mothers (F_0) were grown under control sheltered conditions (table A2). Therefore, the maternal moisture environment significantly affected size (but not age) at reproduction. Compared with siblings (F_1) grown in control unsheltered conditions, offspring (F_1) grown in double rain conditions whose mothers (F_0) were grown in double rain conditions had significantly larger stem diameters (tables 1, 3). Similarly, offspring (F_1) grown under no rain conditions whose mothers (F_1) were also grown in no rain conditions grew significantly larger stem diameters than siblings grown in no rain conditions (tables 1, 3). Therefore, offspring moisture environment also significantly affected size (but not age) at reproduction.

Discussion

Much research effort has focused on the effect of genetic diversity (within or between species) and within-generation phenotypic plasticity on the success of species invasions (Richards et al. 2006; Dlugosch and Parker 2008). Less research has explored the relative importance of abiotic differences between the source environment and recipient environment and the relationship of these differences to successful establishment of invading populations (Sakai et al. 2001; Dietz and Edwards 2006; Dyer et al. 2010). Our results suggest that relatively drier maternal moisture environments can reduce offspring fitness and therefore propagule pressure by influencing plastic responses that are disadvantageous in new environments (e.g., reduced seed biomass in offspring and grandoffspring generations, smaller size at reproduction, and reduced fecundity). By

contrast, increasingly moist maternal environments can increase offspring fitness by generating plastic responses that are advantageous in less moist environments (e.g., increased fecundity and size at reproduction). Our results are consistent with the hypothesis that the invasiveness of weeds is heavily influenced by the source environment (e.g., Dyer et al. 2010; Murren and Dudash 2012).

Mothers' Environment Influences Provisioning of Their Offspring

Broadly, plants grown in resource-rich environments (such as elevated atmospheric CO_2, full sunlight, or moist soil) tend to produce larger seeds than plants grown in resource-poor environments (Stratton 1989; Miao et al. 1991; Sultan 1996). Here, the offspring of double rain mothers (either 2010 or 2011) were not significantly heavier than those produced by control sheltered plants. However, mothers grown in no rain environments tended to produce lighter offspring than the mothers grown under control sheltered or control unsheltered conditions, and these effects may persist for at least two generations. Similar results have been demonstrated in the close relative *Raphanus sativus*, where plants experiencing water limitations tended to produce smaller, less developed embryos (Diggle et al. 2010). However, maternal moisture environment has not necessarily resulted in modified seed biomass in every plant species tested (e.g., *Lupinus perennis* [Halpern 2005], *Polygonum persicaria* [Sultan 1996]) or may have the opposite effects, where seed biomass decreases with increasing moisture availability (e.g., *Sinapis arvensis*; Luzuriaga et al. 2006). Apparently, maternal *Raphanus* plants with limited soil moisture provision offspring less than mothers in more resource-abundant environments. Moreover, we observed that increasing water availability over and above that provided by control conditions (i.e., double rain conditions) did not increase offspring biomass. We hypothesize that below a threshold soil moisture, *Raphanus* mothers flexibly adjust their offspring provisioning.

Mothers' Environment Influences the Invasiveness of Offspring

Offspring of double rain mothers produced more seeds per fruit and seeds per plant relative to those offspring produced

by control sheltered mothers (fig. 4). Differences in number of flowers produced per plant or selective abortion of fruits in response to environmental variation may explain these fitness differences (Marshall and Ellstrand 1988). Water-rich source populations may grow more quickly—if population growth is limited by seed availability—than when migrant offspring come from source populations in relatively dry environments (fig. 4). This corroborates previous findings indicating that globally successful invasive plant species, regardless of the type of environment they invade, tend to come from resource-rich native environments (Dostál et al. 2013).

Furthermore, the recipient environment also affected the tendency of offspring to be invasive (fig. 4). In other scenarios, the recipient environment could be relatively similar to the maternal environment, such as when offspring disperse short distances, or radically different, when offspring disperse long distances (Broennimann et al. 2007; Skarpaas and Shea 2007; Von der Lippe and Kowarik 2007). For offspring from the no rain maternal environment, when grown in control unsheltered conditions, they had higher fecundity than siblings that were grown under a second generation of no rain treatment. By contrast, plants grown under control sheltered conditions for two generations had higher fecundity than offspring transplanted into control unsheltered conditions. Apparently, when the offspring environment had increased water availability, offspring themselves were able to compensate for shortcomings inherited from their resource-limited mother. These results can contribute to modifications of models predicting biological invasions. Anticipating future distributions of invasive species has often relied on niche-based models (e.g., beetles [Peterson and Vieglais 2001], fish [Chen et al. 2007], birds [Peterson et al. 2003], plants [Thuiller et al. 2005]). Our work suggests that these models must not only consider the recipient environment (and its similarity to source environments) but also account for transgenerational responses to those differences in predicting invasion outcomes.

The major limitation of our study was being unable to create a fully reciprocal transplant design across generations owing to border restrictions between the United States and Canada. However, we were still able to challenge offspring (F_1) with the moisture conditions experienced by their maternal parent or a single environmental alternative (control unsheltered). A fully reciprocal transplant experiment should be a priority for future work once sufficient resources are available. Further, invasion of an area with different soil characteristics, latitudes, and presumably microbial communities may have influenced our results in unknown ways; future work should attempt to quantify such factors to provide a greater understanding of the complexity related to invasion success.

Life History Traits Responded to Generational Differences in Environment

Variation in life history traits makes crucial contributions to the relative success of *Raphanus* (Campbell and Snow 2007; Campbell et al. 2009). Generally, large plants that start flowering relatively early produce more flowers and ultimately more seeds than either small or late-flowering plants. Our results show that inherited developmental effects of abundant water availability in *Raphanus raphanistrum* enhanced specific traits (e.g., stem diameter) that contribute to the success of offspring in drier conditions. This is consistent with recent results in *Mimulus*, where maternal effects influenced the stem diameter and, more broadly, the size to subsequently increase the invasiveness of plants, especially in novel sites with environmental conditions that typically support this species (Murren and Dudash 2012). Therefore, we predict that propagules migrating from a relatively wet environment may be more successful at invading relatively drier environments. The substantial provisioning benefit of larger size that resulted from a relatively wet maternal environment would be particularly beneficial in drier environments where belowground competition may be more intense (Pugnaire and Luque 2001). Furthermore, plants with larger stem diameters can also sustain more fruits and grow out of larger root systems, which could reach soil depths where moister soil conditions occur (Campbell et al. 2009). As we have demonstrated here, relative differences in the mean value of key life history traits that plastically respond to a range of environmental conditions (both within and between generations) can provide a powerful tool to explore the weediness of agricultural pests and thus provide mechanistic explanations of colonization events, especially those that involve changes in environmental conditions.

Literature Cited

Axmanova I, D Zeleny, C-F Li, M Chytry 2011 Environmental factors influencing herb layer productivity in central European oak forests: insights from soil and biomass analyses and a phytometer experiment. Plant Soil 342:183–194.

Baker HG, GL Stebbins 1965 The genetics of colonizing species. Academic Press, New York.

Beaton LL, SA Dudley 2010 Maternal effects and drought tolerance determine seedling establishment success in a common roadside plant, *Dipsacus fullonum* subsp. *sylvestris*. Botany 88:930–936.

Bezemer TM, TH Jones 2012 The effects of CO_2 and nutrient enrichment on photosynthesis and growth of *Poa annua* in two consecutive generations. Ecol Res 27:873–882.

Broennimann O, UA Treier, H Müller-Schärer, W Thuiller, AT Peterson, A Guisan 2007 Evidence of climatic niche shift during biological invasion. Ecol Lett 10:701–709.

Brooks ML, CM D'Antonio, DM Richardson, JB Grace, JE Keeley, JM DiTomaso, RJ Hobbs, et al 2004 Effects of invasive alien plants on fire regimes. Bioscience 54:677–688.

Burgess KS, M Morgan, L Deverno, BC Husband 2005 Asymmetrical introgression between two *Morus* species (*M. alba*, *M. rubra*) that differ in abundance. Mol Ecol 14:3471–3483.

Campbell LG, AA Snow 2007 Competition alters life history and increases the relative fecundity of crop-wild radish hybrids (*Raphanus* spp.). New Phytol 173:648–660.

Campbell LG, AA Snow, CE Ridley 2006 Weed evolution after crop gene introgression: greater survival and fecundity of hybrids in a new environment. Ecol Lett 9:1198–1209.

Campbell LG, AA Snow, PM Sweeney 2009 When divergent life histories hybridize: insights into adaptive life-history traits in an annual weed. New Phytol 184:806–818.

Chen PF, EO Wiley, KM McNyset 2007 Ecological niche modeling as a predictive tool: silver and bighead carps in North America. Biol Invasions 9:43–51.

Conner JK, S Via 1993 Patterns of phenotypic and genetic correlations among morphological and life-history traits in wild radish, *Raphanus raphanistrum*. Evolution 47:704–711.

Ctvrtlikova M, P Znachor, J Nedoma, J Vrba 2012 Effects of temperature on the phenology of germination of *Isoetes echinospora*. Preslia 84:141–153.

Dietz H, PJ Edwards 2006 Recognition that causal processes change during plant invasion helps explain conflicts in evidence. Ecology 87:1359–1367.

Diggle PK, NJ Abrahamson, RL Baker, MG Barnes, TL Koontz, CR Lay, JS Medeiros, et al 2010 Dynamics of maternal and paternal effects on embryo and seed development in wild radish (*Raphanus sativus*). Ann Bot 106:309–319.

Dlugosch KM, IM Parker 2008 Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Mol Ecol 17:431–449.

Donohue K 2009 Completing the cycle: maternal effects as the missing link in plant life histories. Philos Trans R Soc B 364: 1059–1074.

Donohue K, J Schmitt 1998 Maternal environmental effects in plants: adaptive plasticity? Pages 137–158 *in* TA Mousseau, CW Fox, eds. Maternal effects as adaptations. Oxford University Press, Oxford.

Dostál P, J Müllerová, P Pyšek, J Pergl, T Klinerová 2013 The impact of an invasive plant changes over time. Ecol Lett 16:1277–1284.

Drescher M, SC Thomas 2013 Snow cover manipulations alter survival of early life stages of cold-temperate tree species. Oikos 122: 541–554.

Drew RLK, PA Brocklehurst 1990 Effects of temperature of mother-plant environment on yield and germination of seeds of lettuce (*Lactuca sativa*). Ann Bot 66:63–71.

Dukes JS, HA Mooney 2004 Disruption of ecosystem processes in western North America by invasive species. Rev Chil Hist Nat 77: 411–437.

Dyer AR, CS Brown, EK Espeland, JK McKay, H Meimberg, KJ Rice 2010 The role of adaptive trans-generational plasticity in biological invasions of plants. Evol Appl 3:179–192.

Environment Canada 2011 National climate data and information archive. http://climate.weather.gc.ca/.

Gallien L, T Münkemüller, CH Albert, I Boulangeat, W Thuiller 2010 Predicting potential distributions of invasive species: where to go from here. Divers Distrib 16:331–342.

Galloway LF, JR Etterson 2009 Plasticity to canopy shade in a monocarpic herb: within- and between-generation effects. New Phytol 182:1003–1012.

Gimeno TE, B Pias, JP Lemos-Filho, F Valladares 2009 Plasticity and stress tolerance override local adaptation in the responses of Mediterranean holm oak seedlings to drought and cold. Tree Physiol 29: 87–98.

Goodwin BJ, AJ McAllister, L Fahrig 1999 Predicting invasiveness of plant species based on biological information. Conserv Biol 13: 422–426.

Halpern SL 2005 Sources and consequences of seed size variation in *Lupinus perennis* (Fabaceae): adaptive and non-adaptive hypotheses. Am J Bot 92:205–213.

Hedhly A, JI Hormaza, M Herrero 2009 Global warming and sexual plant reproduction. Trends Plant Sci 14:30–36.

Holm LG, J Doll, E Holm, J Panch, J Herberger 1997 World weeds: natural histories and distributions. Wiley, New York.

Hovick SM, LG Campbell, AA Snow, KD Whitney 2012 Hybridization alters early life-history traits and increases plant colonization success in a novel region. Am Nat 179:192–203.

Hoyle GL, SE Venn, KJ Steadman, RB Good, EJ McAuliffe, ER Williams, AB Nicotra 2013 Soil warming increases plant species richness but decreases germination from the alpine soil seed bank. Glob Change Biol 19:1549–1561.

Kim E, K Donohue 2013 Local adaptation and plasticity of *Erysimum capitatum* to altitude: its implications for responses to climate change. J Ecol 101:796–805.

Lacey EP, D Herr 2000 Parental effects in *Plantago lanceolata* L. III. Measuring parental temperature effects in the field. Evolution 54: 1207–1217.

Latzel V, J Klimesova, T Hajek, S Gomez, P Smilauer 2010 Maternal effects alter progeny's response to disturbance and nutrients in two *Plantago* species. Oikos 119:1700–1710.

Levine JM, M Vila, CM D'Antonio, JS Dukes, K Grigulis, S Lavorel 2003 Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc B 270:775–781.

Li Y, H Yang, J Xia, W Zhang, S Wan, L Li 2011 Effects of increased nitrogen deposition and precipitation on seed and seedling production of *Potentilla tanacetifolia* in a temperate steppe ecosystem. PLoS ONE 6:e28601.

Luzuriaga AL, A Escudero, F Perez-Garcia 2006 Environmental maternal effects on seed morphology and germination in *Sinapis arvensis* (Cruciferae). Weed Res 46:163–174.

Mack RN 1995 Understanding the processes of weed invasions: the influence of environmental stochasticity. Pages 65–76 *in* CH Stirton, ed. Weeds in a Changing World 64. British Crop Protection Council, Brighton.

Marshall DL, NC Ellstrand 1988 Effective mate choice in wild radish: evidence for selective seed abortion and its mechanism. Am Nat 131:739–756.

Meineri E, J Spindelbock, V Vandvik 2013 Seedling emergence responds to both seed source and recruitment site climates: a climate change experiment combining transplant and gradient approaches. Plant Ecol 214:607–619.

Miao SL, FA Bazzaz, RB Primack 1991 Effects of maternal nutrient pulse on reproduction of two colonizing *Plantago* species. Ecology 73:586–596.

Monty A, J Lebeau, P Meerts, G Mahy 2009 An explicit test for the contribution of environmental maternal effects to rapid clinal differentiation in an invasive plant. J Evol Biol 22:917–926.

Murren CJ, MR Dudash 2012 Variation in inbreeding depression and plasticity across native and non-native field environments. Ann Bot 109:621–632.

Norkko J, DC Reed, K Timmermann, A Norkko, BG Gustafsson, E Bonsdorff, CP Slomp, J Carstensen, DJ Conley 2012 A welcome can of worms? hypoxia mitigation by an invasive species. Glob Change Biol 18:422–434.

Pauchard A, K Shea 2006 Integrating the study of non-native plant invasions across spatial scales. Biol Invasions 8:399–413.

Peterson AT, M Papes, DA Kluza 2003 Predicting the potential invasive distributions of four alien plant species in North America. Weed Sci 51:863–868.

Peterson AT, DA Vieglais 2001 Predicting species invasions using ecological niche modelling: new approaches from bioinformatics attack a pressing problem. Bioscience 51:363–371.

Pugnaire FI, MT Luque 2001 Changes in plant interactions along a gradient of environmental stress. Oikos 93:42–49.

Rejmánek M, DM Richardson 1996 What attributes make some plant species more invasive? Ecology 77:1655–1661.

Rhymer JM, D Simberloff 1996 Extinction by hybridization and introgression. Annu Rev Ecol Syst 27:83–109.

Richards CL, O Bossdorf, NZ Muth, J Gurevitch, M Pigliucci 2006 Jack of all trades, master of some? on the role of phenotypic plasticity in plant invasions. Ecol Lett 9:981–993.

Riginos C, MS Heschel, J Schmitt 2007 Maternal effects of drought stress and inbreeding in *Impatiens capensis* (Balsaminaceae). Am J Bot 94:1984–1991.

Sakai AK, FW Allendorf, JS Holt, DM Lodge, J Molofsky, KA With, S Baughman, et al 2001 The population biology of invasive species. Annu Rev Ecol Syst 32:305–332.

Skalova H, L Moravcova, P Pysek 2011 Germination dynamics and seedling frost resistance of invasive and native *Impatiens* species reflect local climatic conditions. Perspect Plant Ecol Evol Syst 13: 173–180.

Skarpaas O, K Shea 2007 Dispersal patterns, dispersal mechanisms, and invasion wave speeds for invasive thistles. Am Nat 170:421–430.

Sneck MA 2013 Evolutionary responses to global change: an experimental test of the effect of altered precipitation on hybridization rates in sunflower (Helianthus). MA thesis. Rice University, Houston, TX.

Stratton DA 1989 Competition prolongs expression of maternal effects in seedlings of *Erigeron annus* (Asteraceae). Am J Bot 76: 1646–1653.

Sultan SE 1996 Phenotypic plasticity for offspring traits in *Polygonum persicaria*. Ecology 77:1791–1807.

Theoharides KA, JS Dukes 2007 Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273.

Thuiller W, DM Richardson, P Pysek, GF Midgley, GO Hughes, M Rouget 2005 Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Glob Change Biol 11: 2234–2250.

van Oldenborgh GJ, G Burgers 2005 Searching for decadal variations in ENSO precipitation teleconnections. Geophys Res Lett 32. doi:10.1029/2005GL023110.

Vermeij GJ 2005 Invasion as expectation. Pages 315–339 *in* DF Sax, JJ Stachowicz, SD Gaines, eds. Species invasions: insights into ecology, evolution and biogeography. Sinauer, Sunderland, MA.

Von der Lippe M, I Kowarik 2007 Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv Biol 21:986–996.

Warwick SI, A Francis 2005 The biology of Canadian weeds. 132. *Raphanus raphanistrum* L. Can J Plant Sci 85:709–733.

Whitney KD, CA Gabler 2008 Rapid evolution in introduced species, "invasive traits" and recipient communities: challenges for predicting invasive potential. Divers Distrib 14:569–580.

Widmer TL, F Guermache, MY Dolgovskaia, SY Reznik 2007 Enhanced growth and seed properties in introduced vs. native populations of yellow starthistle (*Centaurea solstitialis*). Weed Sci 55: 465–473.

Yahdjian L, OE Sala 2002 A rainout shelter design for intercepting different amounts of rainfall. Oecologia 133:95–101.

Zhang R, RS Gallagher, K Shea 2012 Maternal warming affects early life stages of an invasive thistle. Plant Biol 14:783–788.