Maternal Environment Influences Propagule Pressure of an Invasive Plant, *Raphanus raphanistrum* (Brassicaceae)

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

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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 Moomaw 2004; Norkko et al. 2012), and compromising native genomes via hybridization with neighbors (Rhymers 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-
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 Etter 2012; 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 (F0). The maternal generation experiment was established at Waterman Farm, Columbus, Ohio (lat. 40° 79′ 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 (F1) 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 831.5 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 (F0) Experiment

To measure the traits of two generations of R. raphanistrum with experimentally altered soil moisture, F0 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 (F1) experiment, detailed below and in figure 1B, 1C.

For this first generation, seeds from more than 200 F0 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 Helenium annuum, and nine Helenium 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 F1 offspring produced by the F0 R. raphanistrum plants were used in this study. We did not receive permission to import the offspring of R. sativus, H. annuum, or H. petiolaris to Canada, and therefore these three species were not planted in the F1 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-

Fig. 1 Schematic of experiments to quantify effect of maternal soil moisture environment on phenotype of offspring and grandoffspring. A. For the maternal generation (F0) 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 F0 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 (F1) experiment performed in King City, Ontario, 20 offspring (F2) 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 (F2) per F1 plant grown in B and C were extracted from fruits and weighed (600 seeds total). All data except F0 soil moisture and seed biomass and F2 seed biomass were taken on F1 plants.
unpublished manuscript), and all hybrid offspring (9 of 800)
bridization rate was very low (80x436). 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 experimen-
tal 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 mater-
nal generation (F0) 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 hybrid-
ization 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 genera-
tion (F1) by their white flowers, were excluded from the ex-
periment. We collected up to 18 fruits from the four central,
maternal generation (F0) 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 be-
cause their relaxed and variable competitive environments may
have altered maternal moisture environments for the seeds pro-
duced on the plants.

Offspring Generation (F1) Experiment
The control unsheltered treatment represented a new off-
spring moisture environment relative to the maternal environ-
ment experienced by the control sheltered, no rain, and double
rain maternal generation (F0) plants. Thus, we considered the
relative success of F1 offspring plants growing in this novel environ-
ment to be indicative of their response to a newly col-
onized 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 mater-
nal generation (F0) control unsheltered to offspring generation
(F1) control unsheltered or from maternal generation (F0) no
rain to offspring generation (F1) no rain).

To plant the offspring generation (F1) experiment, we used
the offspring from 12 randomly chosen maternal environment
plots—three replicate plots from each treatment. 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 allo-
cated to replicate plots within the moisture environment ex-
perienced by their maternal parent or to replicate control un-
sheltered moisture environment plots. While we kept track of
half-sib families for the purpose of planting plots and repli-
cates 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 lim-
ited 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 con-
tral sheltered plots and double the amount that had fallen
as rain in double rain plots. In each of the 40 offspring gen-
eration (F1) experiment plots, we planted four rows of five
plants with 20 cm between plants (fig. 1C). Each plot was sur-
ronded 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 nat-
ural 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 sin-
gle soil moisture reading was taken from the center of each
plot. For every subsequent sampling period, average soil mois-
ture 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 approx-
imately 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 (F1), so all data on plant traits except
F0 and F2 seed biomass were collected on that generation. Given
that maternal environment may be reflected early in plant life

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cycles, we recorded mass of seeds produced by a subset of maternal F₀ plants (four of nine in each plot). We weighed five seeds per fruit to a maximum of 90 F₁ seeds per maternal plant (i.e., seeds from up to 18 fruits).

For each offspring F₁ 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. 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 F₁, 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 F₀ 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 days to flowering, stem diameter, log number of fruits per plant, seeds per fruit, and log of total number of seeds per plant. To examine the immediate effects of the maternal generation experiment on F₁ seed biomass, we used a repeated-measures mixed-model ANOVA with an autoregressive covariance matrix that included the maternal (F₀) 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 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 F₀ 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 F₁ 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 F₂ seed biomass, we used a linear mixed-model ANOVA, which included the offspring (F₁) watering treatment as a fixed effect. This was done two ways: we performed (i) three sub-analyses that held maternal F₀ environment constant and compared paired offspring treatments to understand the effect of the offspring environment (F₁) on F₂ traits and F₂ seed biomass (table 1) and (ii) a sub-analysis with data from only those plots that were grown under offspring (F₁) control unsheltered conditions to hold offspring generation environment constant while the maternal generation environment varied to understand the effect of the maternal environment (F₀) on F₂ seed biomass (table A2).

c) Cumulative environmental effects. Finally, to compare the degree of phenotypic differences of plants grown under the
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 sheltered and control unsheltered 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 (F0) significantly altered offspring (F1) seed biomass (table A3). F1 seeds produced in maternal generation (F0) no rain plots weighed less than those produced in the maternal generation control unsheltered or control sheltered plots (fig. 3A). Similarly, experimental watering of the offspring generation (F1) significantly altered grandoffspring seed biomass (tables 1, 2; fig. 3B). Further, F2 seeds from plants grown under both maternal generation (F0) and offspring generation (F1) no rain plots were significantly lighter than F2 seeds produced in all other plots (fig. 3B). Experimental watering in the F0 maternal generation also had a significant effect on F2 seed biomass (table A2); plants in control unsheltered conditions produced

<table>
<thead>
<tr>
<th>Table 1</th>
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<tr>
<td>Effects of the Application of Maternal (F0) or Control Unsheltered Watering Treatments on the Raphanus raphanistrum Offspring Phenotype (F1) When Sharing a Common Maternal Environment</td>
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<tr>
<td></td>
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<tr>
<td>Log10 (days to flowering)</td>
</tr>
<tr>
<td>Stem diameter</td>
</tr>
<tr>
<td>Log10 (fruit no.)</td>
</tr>
<tr>
<td>Seeds per fruit</td>
</tr>
<tr>
<td>Log10 (total no. seeds)</td>
</tr>
<tr>
<td>F2 seed biomass</td>
</tr>
</tbody>
</table>

Note. F statistics are given for moisture treatment, a fixed effect (offspring generation [F1] environment). CS = control sheltered, DR = double rain, NR = no rain.

* P < 0.10.
** P < 0.05.
*** P < 0.01.
**** P < 0.001.

<table>
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<tr>
<th>Table 2</th>
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<tr>
<td>Effects of Soil Moisture Environments Consistently Applied for Two Generations (in Both the Maternal Generation [F0] and Offspring Generation [F1] Experiments) on the Fecundity of F1 Raphanus raphanistrum from the Offspring Generation (F1) Experiment</td>
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<td>ANOVA</td>
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<tr>
<td>Log10 (days to flowering)</td>
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<td>Stem diameter</td>
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<tr>
<td>Log10 (no. fruits)</td>
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<tr>
<td>Average no. seeds per fruit</td>
</tr>
<tr>
<td>Log10 (no. seeds per plant)</td>
</tr>
</tbody>
</table>

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.
heavier grandoffspring than plants grown in control sheltered conditions (table A2; fig. 3). Finally, harvest date of seeds had a significant effect on F1 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 (F1) grown under control unsheltered environments whose mothers (F0) were grown under double rain conditions were significantly more fecund than those offspring (F1) whose mothers (F0) were grown under no rain or control sheltered conditions (tables A2, 3). Furthermore, we found that offspring produced in resource-rich environments outperformed plants produced in resource-poor environments when growing in their maternal environment. Offspring (F1) grown under double rain conditions from mothers (F0) grown under double rain conditions produced significantly more fruits and more seeds per plant relative to offspring (F1) grown under control sheltered conditions from mothers (F0) also grown under control sheltered conditions (tables 2, 3). Furthermore, offspring (F1) grown under no rain conditions from mothers (F0) also grown under no rain conditions produced fewer fruits and total seeds per plant relative to offspring (F1) 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).
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 (F1) grown under control unsheltered conditions whose mothers (F0) were grown under either control unsheltered or double rain conditions grew significantly larger stem diameters than offspring (F1) grown under control unsheltered conditions whose mothers (F0) were grown under control sheltered conditions (table A2). Therefore, the maternal moisture environment significantly affected size (but not age) at reproduction. Compared with siblings (F1) grown in control unsheltered conditions, offspring (F1) grown in double rain conditions whose mothers (F0) were grown in double rain conditions had significantly larger stem diameters (tables 1, 3). Similarly, offspring (F1) grown under no rain conditions whose mothers (F0) 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 by generating plastic responses that are disadvantageous in new environments (e.g., increased fecundity and size at reproduction). 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 CO2, 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

<table>
<thead>
<tr>
<th>Maternal generation (F₀) treatment</th>
<th>Offspring generation (F₁) treatment</th>
<th>Age at flowering (d)</th>
<th>Stem diameter (mm)</th>
<th>Average no. seeds per fruit</th>
<th>No. fruits</th>
<th>No. seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>CU</td>
<td>CU</td>
<td>33.25 (.53)</td>
<td>6.02 (.24)</td>
<td>5.27 (.14)</td>
<td>265.20</td>
<td>1442.30</td>
</tr>
<tr>
<td>CS</td>
<td>CS</td>
<td>33.10 (.32)</td>
<td>5.11 (.31)</td>
<td>5.30 (.16)</td>
<td>233.12</td>
<td>1243.60</td>
</tr>
<tr>
<td>CS</td>
<td>CU</td>
<td>33.48 (.46)</td>
<td>4.71 (.23)</td>
<td>4.91 (.17)</td>
<td>164.68</td>
<td>809.40</td>
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<tr>
<td>NR</td>
<td>NR</td>
<td>32.64 (.45)</td>
<td>5.74 (.19)</td>
<td>5.08 (.15)</td>
<td>145.85</td>
<td>781.35</td>
</tr>
<tr>
<td>NR</td>
<td>CU</td>
<td>33.06 (.49)</td>
<td>5.12 (.20)</td>
<td>5.03 (.17)</td>
<td>193.71</td>
<td>993.02</td>
</tr>
<tr>
<td>DR</td>
<td>DR</td>
<td>32.89 (.77)</td>
<td>6.62 (.22)</td>
<td>5.38 (.17)</td>
<td>360.89</td>
<td>1966.10</td>
</tr>
<tr>
<td>DR</td>
<td>CU</td>
<td>33.00 (.53)</td>
<td>5.88 (.18)</td>
<td>5.67 (.18)</td>
<td>280.43</td>
<td>1737.90</td>
</tr>
</tbody>
</table>

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.
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 Vieglass 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 (F1) with border restrictions between the United States and Canada. 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 Luecke 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 plasticity 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.

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