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Transgenerational effects of parent plant competition on offspring development in contrasting conditions

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Abstract. Conditions during a parent's lifetime can induce phenotypic changes in offspring, providing a potentially important source of variation in natural populations. Yet, to date, biotic factors have seldom been tested as sources of transgenerational effects in plants. In a greenhouse experiment with the generalist annual *Polygonum persicaria*, we tested for effects of parental competition on offspring by growing isogenic parent plants either individually or in competitive arrays and comparing their seedling progeny in contrasting growth environments. Offspring of competing vs. non-competing parents showed significantly altered development, resulting in greater biomass and total leaf area, but only when growing in neighbor or simulated canopy shade, rather than sunny dry conditions. A follow-up experiment in which parent plants instead competed in dry soil found that offspring in dry soil had slightly reduced growth, both with and without competitors. In neither experiment were effects of parental competition explained by changes in seed provisioning, suggesting a more complex mode of regulatory inheritance. We hypothesize that parental competition in moist soil (i.e., primarily for light) confers specific developmental effects that are beneficial for light-limited offspring, while parental competition in dry soil (i.e., primarily for belowground resources) produces offspring of slightly lower overall quality. Together, these results indicate that competitive conditions during the parental generation can contribute significantly to offspring variation, but these transgenerational effects will depend on the abiotic resources available to both parents and progeny.

Key words: non-genetic inheritance; parental effects; plant density; Polygonum persicaria*; seed provisioning; transgenerational plasticity.*

INTRODUCTION

In recent years, there has been increasing interest in whether parental environments can contribute importantly to phenotypic variation in offspring (Mousseau et al. 2009, Sultan 2015, Bonduriansky and Day 2018, Uller 2019). Inherited environmental effects (often termed "transgenerational plasticity," "parental/maternal effects," or "non-genetic inheritance") have been documented in organisms across all kingdoms of life, induced by a variety of abiotic and biotic environmental cues (reviewed by Jablonka and Raz 2009, Salinas et al. 2013). Such transgenerational effects may passively reflect maternal nutritional status if limited resource provisioning to seeds or eggs constrains offspring growth or if greater offspring provisioning results in overall growth increases (Roach and Wulff 1987, Grafen 1988, Fenner and Thompson 2005*a*). In other cases, transgenerational plasticity may be adaptive or "anticipatory" (Marshall and Uller 2007); in such cases, parental exposure to an environmental cue induces specific changes to offspring trait expression that increase fitness in environments associated with that cue (reviewed by Auge et al. 2017, Bonduriansky and Day 2018, Donelson et al. 2018).

Like other aspects of phenotypic plasticity, transgenerational effects have been intensively studied in plants (reviewed by Herman and Sultan 2011), reflecting the relative feasibility of creating genetically uniform (isogenic) replicate parent plants to precisely assess the developmental impact of alternative environments. Although natural habitats comprise complex combinations of biotic and abiotic factors (Bazzaz 1996, Suzuki et al. 2014), most prior plant studies have tested the effects on offspring of contrasting levels of a single, usually abiotic aspect of the parental environment such as temperature, light, or moisture (e.g., 22 of the 26 plant studies cited by Salinas et al. 2013). Less information is known about the potential inherited effects of biotic factors that characterize plant habitats (Puy et al. 2021), apart from herbivory (reviewed by Holeski et al. 2012), or about how these effects may be influenced by co-occurring abiotic conditions such as soil resource levels. In particular, intraspecific competition is a key biotic

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stress in natural populations (Tilman and May 1988, Adler et al. 2018).

At high densities, plants compete aboveground for light and belowground for water and nutrients (Goldberg 1990, Bazzaz 1996, Craine and Dybzinski 2013). The relative severity of aboveground and belowground competitive stresses also depends on soil conditions (Cahill 2002, Foxx and Fort 2019). While plants with ample soil resources often produce large shoot systems and compete primarily for light, dry soil limits access to both water and nutrients, which generally causes greater investment in root systems and more intense belowground competition (Fitter and Hay 1987). In addition to influencing individual seedling establishment and survival (Fenner and Thompson 2005*b*, Fayolle et al. 2009), these competition-based resource stresses shift and interact in complex ways across the lifecycle according to dynamic growth responses of competing neighbors (Coelho et al. 2000, Schmitt et al. 2003, Burns and Strauss 2012).

The well established literature on within-generation growth effects of competition includes several studies showing that an individual's competitive performance can be reduced if its parents faced drought, nutrient stress, or herbivory (Stratton 1989, Van Dam and Baldwin 2001, Metz et al. 2015). Yet, to date, few studies in natural systems have tested the potential transgenerational effects of competitive intensity during the parent generation on offspring, and all but one of the existing studies are limited to effects on seed traits rather than offspring phenotypes. The results of the seed studies are quite variable depending on the particular type of competitive stress and the study species, finding for example both negative and positive effects of parental competition on seed mass (Mazer and Wolfe 1992, Platenkamp and Shaw 1993, Germain et al. 2019) and germination (Violle et al. 2009, Leverett et al. 2018). Although the results of these seed studies are not consistent, they indicate a potential transgenerational impact of parental competition on ecologically important offspring traits. The one prior study that investigated parental competitive effects beyond the earliest life stage found that offspring phenotypes were indeed altered when parents had faced more intense competition, expressing growth traits such as accelerated development that were inferred to promote their competitive ability (Puy et al. 2021). However, because these findings were based on a single genotype of an apomictic perennial, it remains unclear whether they apply more broadly, in particular to sexually reproducing taxa in which transgenerational signals must persist through meiosis (note that only an estimated 1% of angiosperms are substantially apomictic; Whitton et al. 2008). Moreover, because competition imposes stresses differently in dry vs. moist soil, any developmental effects of parental competition on progeny may be influenced by parental soil conditions. Indirect support for this idea is provided by experiments finding that neighbor identity effects on seeds differ by parental nitrogen treatment (Violle et al. 2009) and soil moisture treatment (Germain et al. 2019). These results provide some support for the possibility that parental competition effects on progeny are influenced by concurrent abiotic stresses experienced by parent plants.

Depending on how they are mediated, transgenerational developmental effects could be expressed in several ways. Parental resource stress due to competition could result in decreased quantity of offspring provisioning (as suggested by cases where parental competition reduces seed mass; Mazer and Wolfe 1992, Platenkamp and Shaw 1993, Dechaine et al. 2015); increased provisioning is also a possible response to certain parental stresses in some systems (Schmitt et al. 1992, Schmid and Dolt 1994, Sultan 1996, 2001, Germain et al. 2013). Parental stresses may also alter seed quality (Wulff 1995). Such positive or negative provisioning changes are expected to, respectively, increase or decrease overall growth of offspring, including initial growth rates (Roach and Wulff 1987, Haig and Westoby 1988, Leishman et al. 2000).

Alternatively, the transgenerational effects of parental competition might be mediated by induced, heritable changes to epigenetic regulatory factors, such as DNA methylation or small non-coding RNAs (reviewed by Hauser et al. 2011, Blake and Watson 2016). Unlike provisioning changes, heritable epigenetic factors induced by the parental environment can cause more targeted changes to specific regulatory pathways, and therefore they may only impact certain traits (Badyaev and Uller 2009, Johannes et al. 2009). Furthermore, because those pathways are also influenced by the developing individual's current environment, this makes possible the developmental integration of parental and progeny environmental effects ("context-dependent effects" *sensu* Baker et al. 2018; see also Verhoeven and van Gurp 2012, McNamara et al. 2016). Such integrated responses may include functionally adaptive, context-specific trait expression when offspring environments match those experienced by parent individuals (Marshall and Uller 2007, Galloway and Etterson 2009, Herman et al. 2014). For example, in one study the progeny of shade-stressed parents produced greater leaf area than those of isogenic full-sun parents, but this developmental change was far more pronounced when the progeny were themselves grown in shade (Baker et al. 2018). Similarly, an epigenetic change induced by parental competition that causes greater offspring stem elongation (therefore avoiding neighbor shading) might only be expressed when offspring are also grown with competitors. In addition to testing offspring in matching conditions, testing offspring in more exaggerated versions of the parental stress can provide further insight into the nature of these effects. For example, Baker et al. (2019) found that the positive effect of parental shade on progeny biomass was greater for progeny growing in more severe shade than parents had experienced than it was for progeny in a competitive treatment that imposed only moderate shade.

To gain insight into possible transgenerational effects of competition, we conducted a two-part study in a naturally evolved system by using a sample of genotypes of the widespread annual *Polygonum persicaria* collected from local populations. This species occurs across broad ranges of both competitive density and soil moisture within and across populations (from 1 individual/m^2 to 900/m^2 and microsite volumetric water content 7–68%, R. Waterman, *unpublished data*; Appendix S1: Figs. S1, S2). First, to test whether parental competition-induced transgenerational effects on progeny phenotypes, we raised isogenic replicate *P. persicaria* parents either individually or with competitors (in moist soil) and studied the development of their offspring from germination through early adulthood. Holding genotype constant allowed us to directly test for effects of parental environment rather than genetic effects on progeny development. Instead of a simple factorial, we tested for parental effects in offspring environments that isolated and enhanced two stresses encountered by competing parents, reduced soil moisture and limited light (for a similar design see Baker et al. 2019). This design allowed us to ask three questions: (1) Does parental competition alter offspring development?, (2) If so, do the effects vary depending on offspring conditions?, and (3) Do any observed context-specific expression of transgenerational effects represent functionally adaptive responses to specific stresses? Because this experiment showed little effect of parental competition on offspring growing in dry soil, we conducted a smaller, follow-up factorial experiment to focus on drought stress as an aspect of the parental environment that can be exacerbated by competition. In this second experiment, competing and noncompeting parents were given limited water and progeny were tested in the same two treatments to address the question: will parental competition for limited water lead to specific, functionally adaptive growth effects on offspring that experience drought stress, and if so, will these effects be greater when that stress is intensified because offspring are competing?

METHODS

Study system

Polygonum persicaria (= *Persicaria maculosa*, Kim et al. 2008) is a predominantly selfing colonizing annual native to Eurasia and naturalized throughout North America (Mitchell and Dean 1978, USDA). Achenes (1-seeded fruits) were collected from four field plants >1 m apart in each of five ecologically distinct Massachusetts populations to sample broadly from the species (DFF, M, MHF, NAT, and TP; site descriptions in Sultan et al. 1998); however, trait variation is not structured by population in this system (Appendix S1: Fig. S3). Achenes were inbred in uniform greenhouse conditions for five generations to produce isogenic lines (from this point forwards "genotypes").

Experiment 1: Effects of parental competition in moist soil

Parental generation.—Achenes from each of six genotypes (2 DFF, 2 M, and 2 TP) were stratified for 6 weeks in distilled water at 4°C to fulfill germination requirements and sown into flats of moist vermiculite (13 May 2017). At the first true leaf stage seedlings were transplanted into 1-L clay pots filled with a 1:1:1 mix of sterilized topsoil: coarse sand (Quikrete®, Atlanta, Georgia, USA): fritted clay (Turface™, Buffalo Grove, Illinois, USA) plus 2.5 g/pot of 15-8-12 NPK granular fertilizer (Mountain Green Fertilizer, Niverville, New York, USA). Replicate plants were assigned randomly to one of two parental greenhouse treatments (Ott and Longnecker 2015): *Parent Solo*—one plant/pot, and *Parent Comp*—one central "target" plant surrounded by six "background" competitors of the same genotype/pot (Fig. 1a). Pots were maintained at field capacity moisture in full sun for *c.* 9 weeks. Self-fertilized achenes from each of the 12 parents were collected, air-dried, and stored at 4°C. As a phytometric indicator of treatment intensity, Parent Comp reduced plant reproductive output by 81–89% (depending on genotype) compared with Parent Solo.

Offspring generation.—Achenes from parent plants representing 12 experimental units (6 genotypes × 2 parental treatments) and five other Parent Solo genotypes (2 NAT and 3 MHF; for use as competitive background plants) were stratified for 5 weeks in distilled water at 4°C (8 May 2018). Five to 10 replicate offspring from each experimental parent were grown in a randomized block split-plot design (Ott and Longnecker 2015). Offspring Treatment (main plot factor) consisted of two Offspring Solo treatments: *Drought* (full sun/dry soil) and *Sev Shade* (severe shade/moist soil), and a Competition (*Comp*) treatment (full sun/moist soil). Parental competition treatment and genotype (subplot factors) were completely randomized within each of 10 replicate blocks, arrayed perpendicular to the major linear gradient of spatial variation in the greenhouse: incident light (see Casler 2020 on blocking principles). We determined the spatial distribution of incident light on which this blocking design was based by taking 18 transects covering the entire growth area in the greenhouse compartment, with eight sensor readings per transect, every day at midday for 7 d (R. Waterman, *unpublished data*). Offspring treatment was imposed in a regular pattern from left to right (rather than randomized along this axis across greenhouse benches) to prevent the heterogeneous edge effects that would result from irregularly interspersed shade tents. Such interspersion would compromise the environmental integrity of the Offspring Competition and Drought treatments, violating the primary criterion for proper blocking by creating severe heterogeneity within blocks. We note that this design leaves open the possibility that offspring treatment was

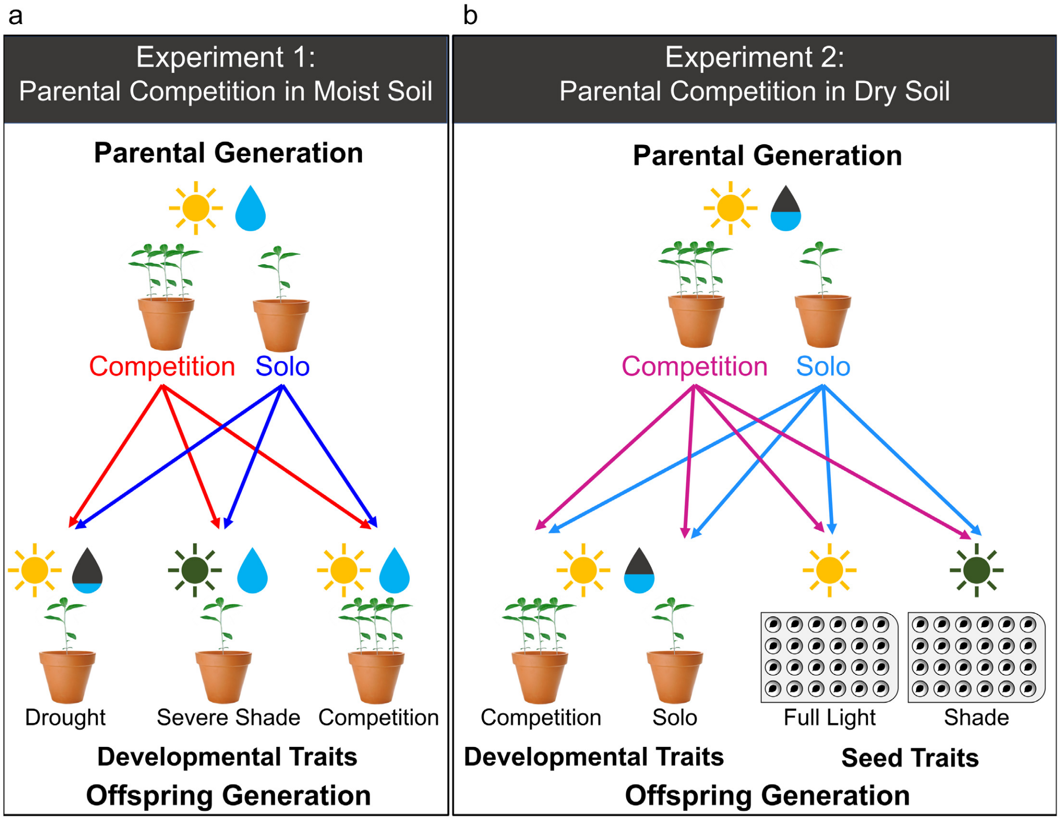

FIG. 1. Experimental design overview. (a) Experiment 1: Effects of Parental Competition vs. Parental Solo for parent plants grown in moist soil on offspring development in three contrasting treatments (Drought—full sun/dry soil; Severe Shade—low PAR and R : FR/moist soil; Competition—full sun/moist soil). Both generations were grown in a greenhouse. (b) Experiment 2: Effects of Parental Competition vs. Parental Solo for parent plants grown in dry soil on offspring development in dry soil/full light with and without competition (Developmental Traits); and on seed mass, offspring germination behavior, and initial germinant mass in Full Light vs. Shade (Seed Traits). The parental generation was grown in a greenhouse and the offspring generation was grown in a growth chamber.

confounded with some unknown variable associated with left vs. right side of the greenhouse compartment. However, measurements of temperature, humidity, airflow, and soil moisture confirm the absence of any spatial gradient from left to right for these environmental parameters (enabled by corner-mounted continuous circulation fans, manual watering of individual pots, and mesh compactor benches forming a contiguous bench area ≥22 h/d).

1. Solo treatments.—Achenes from each experimental parent were sown into vermiculite flats and transplanted as in *Parental generation*, but into 450-mL clay pots (2 July 2018; genotype M6 was dropped from these treatments due to low germination). Drought plants were placed on an open greenhouse bench (mean midday PAR ± SE = 1,455 ± 122 μmol·s^{-1}·m^{-2}) and given equal weather-adjusted daily volumes of water (mean ± SE = 27.5 ± 8.7 mL) such that plants wilted for 1–3 h at midday. Sev Shade plants were placed on a shaded greenhouse bench (mean midday PAR ± SE =52 ± 6 μmol·s^{-1}·m^{-2}) and maintained at field capacity moisture. Simulated shade was provided by 80% neutral-density shade cloth (PAK Unlimited, Cornelia, Georgia, USA) perforated with 3.5-cm-diameter sunfleck holes (Matesanz et al. 2014) overlaid with strips of green plastic filter (no. 138; Lee Filters, Burbank, California, USA) plus an additional layer of 30% neutral-density shade cloth.

2. Competition treatment.—Achenes from each experimental parent were sown into 15-cm Petri dishes lined with moistened filter paper (17 June 2018) and individually transplanted on their day of germination into 450-mL clay pots filled as above. Each central target plant was surrounded by one plant from each of the five background genotypes. Pots were placed on an open greenhouse bench (mean midday PAR ± SE = 1,195 ± 83 μmol·s^{-1}·m^{-2}) and maintained at field capacity moisture. Due to delayed germination in certain genotypes, blocks 1–4 and blocks 5–7 were set up as two temporal blocks.

Data collection.—1. Propagule/seed traits.—A subsample of 40 achenes per experimental unit was collectively weighed to estimate mean individual achene mass of achenes produced by the experimental parents. Emergence percentage was quantified 10 d after sowing as cumulative number of emerged seedlings out of 35 achenes sown into flats.

2. Offspring developmental traits.—For Offspring Comp, traits were measured only on target plants. Seedling height (soil level to apex) was measured every 5 d, 3–6 times depending on treatment (see Waterman 2019 for details). Canopy area was estimated from digitized overhead photographs (Nikon D50 DSLR; Easy Leaf Area V2 software, Easlon and Bloom 2014) taken every 5 d starting 8 d after transplant (not measured in Offspring Comp due to overlapping target and background leaves). After 33 d in treatment, plants were harvested by severing the root-shoot junction. The 2–3 most recent fully expanded leaves were photographed or scanned (LI-3100 Area Meter, LICOR Inc., Lincoln, Nebraska, USA) and weighed to estimate specific leaf area (SLA; leaf area/leaf mass); leaves and stems were separately weighed; and total leaf area was estimated as total leaf mass × SLA. Root systems were hand-washed, air-dried ($\geq$24 h), oven dried (65°C for $\geq$24 h), and weighed (not measured in Offspring Comp due to entangled target and background plant roots). For each Offspring Comp pot, background plant shoots were collectively weighed to calculate the ratio of target plant shoot mass/total pot shoot mass. The final offspring sample was N = 259 (2 parental treatments × 3 offspring treatments × 5–6 genotypes × 5–10 replicate individuals—1 outlier >1.5 × IQR and two seedling deaths).

Experiment 2: Effects of parental competition in dry soil

Parental generation.—Achenes from the six genotypes in Expt. 1 (except with genotype M9 replacing the poorly-germinating M6) were stratified in distilled water at 4°C for 6 weeks, sown into 15-cm Petri dishes lined with moist filter paper (24 June 2019), and transferred to vermiculite flats on their day of germination. Seedlings that had germinated on the same day were transplanted at the first true leaf stage into 1-L clay pots filled with 1:1:1 soil mix (see Expt. 1) in one of two randomly assigned parental greenhouse treatments (Fig. 1b). In *Parent Solo*, each of three replicate plants per genotype was grown without neighbors. In *Parent Comp*, each of five replicate target plants per genotype was surrounded by one background plant from each of the five other experimental genotypes. The same daily volume of water was given to all pots, such that most Parent Comp plants wilted at midday. After *c.* 8 weeks in treatment, self-fertilized achenes were collected, air-dried, and stored at 4°C. Shoot mass was oven dried (100°C for $\geq$1 h then 65°C for $\geq$24 h) and weighed. As a phytometric indicator of treatment intensity, Parent Comp reduced shoot mass by 68–84% and reproductive output by 53–87% (depending on genotype) compared with Parent Solo.

Offspring generation.—1. Treatments: Propagule/seed traits.—Mean individual mass of achenes produced by parents was estimated as in Expt. 1 (N = 100/parent). Based on initial results from Experiment 1 suggesting possible parental effects on achene mass and germination timing, we examined seed traits in detail on a subsample of 20 achenes from each experimental unit (6 genotypes × 2 parental treatments × 20; N = 240). Air-dried achenes were individually weighed, stratified in distilled water at 4°C for 7 weeks, sown into 24-well microplates lined with moist filter paper (18 March 2020), and randomly assigned to one of two growth chamber germination treatments (E-7 dual Conviron customized for enhanced light intensity, Controlled Environments Ltd., Winnipeg, Manitoba, Canada with 23°C:18°C, 14:10 h day : night cycle). In the *Full Light* treatment achenes received *c.* 500 $\mu mol \cdot s^{-1} \cdot m^{-2}$ daytime PAR (SQ-420; Apogee Instruments, Logan, Utah, USA) with red : far-red ratio (R : FR) of 1.9 (SKR 110; Skye Instruments, Llandrindod Wells, UK). In the *Shade* treatment (c. 224 $\mu mol \cdot s^{-1} \cdot m^{-2}$ at R : FR of 1.4), trays were placed under a 30% neutral-density shade cloth lined with green plastic filter with 1-cm sunfleck holes.

2. Treatments: Offspring developmental traits.—Due to logistical constraints including seasonal timing of this follow-up experiment, offspring were grown in a growth chamber, necessitating smaller pots and a slightly shorter measurement period than in Expt. 1. Previous studies in this system and growth chamber confirm that developmental responses to both drought stress and shade are consistent with those in the greenhouse (Sultan et al. 2009, Herman et al. 2012, Baker et al. 2018). Achenes from each experimental unit were stratified, sown (7 November 2019), and transplanted as in Expt. 1: Offspring Comp, but into 200-mL pots. Ten replicate achenes were randomly assigned to each of two offspring treatments: *Solo*—1 plant per pot, and *Comp*—1 central target plant surrounded by four background competitors (2 mol/L and 2 TP Parent Solo offspring). Pots were spatially interspersed in 10 blocks across two growth chamber compartments in full light (see Propagule/Seed Traits) and received equal daily volumes of water (mean c. 25 mL) such that Comp pots were water stressed (*c.* 53% field capacity moisture, R. Waterman, *unpublished data*).

Data collection.—1. Propagule/seed traits.—Cumulative germination percentage (based on all achenes sown, N = 5,080) was recorded 9 d after sowing. For the achene subsample (N = 240), germination was recorded every 2 h during each 14-h daylight period until no new germination occurred for 1 d, and seed provisioning was calculated as achene mass—pericarp mass (collected after germination). To show the combined growth impact of germination timing and initial growth rate, individual germinants were harvested 7 d after sowing, oven dried (at 65°C for ≥24 h), and weighed. Final samples were N = 170 (germination) and N = 167 (provisioning and seedling mass, due to two outliers >1.5 × IQR and one lost pericarp).

2. Developmental traits.—For Offspring Comp, traits were measured only on target plants. On days 7, 14, and 21 after transplant, seedling height was measured and canopy area estimated from digitized overhead photographs (D3100 DSLR, Nikon Instruments, Melville, New York, USA; ImageJ® software). Seedlings were harvested 21 d after transplant (2 December–7 December 2019). For each seedling, the two most recent fully expanded leaves were used to estimate SLA (see Expt. 1), and the oven-dried target and background shoot and root systems were weighed. All traits were measured as in Expt. 1, except roots were scanned prior to drying (Epson Perfection V800 at 1200 DPI). Total root length was estimated using RootGraph software (Cai et al. 2015). Specific root length was estimated as total root length/root mass. Final samples were N = 235 (228 for root-based traits; 2 parental treatments × 2 offspring treatments × 6 genotypes × 9–10 replicate individuals—8 outliers >1.5 × IQR, two deaths, and seven root losses).

Data analysis (both experiments)

Analyses were performed using JMP® Pro 14 (SAS Institute, Cary, North Carolina, USA) and plots created in R v.3.6.3 (R Core Development Team 2020) except for survival analyses, which were performed and plotted using the PHREG and ICLIFETEST procedures in SAS® 9.4 (SAS Institute). For post-hoc tests, possible Type I error due to multiple comparisons was controlled using the Benjamini-Hochberg method with a 5% false discovery rate (Benjamini and Hochberg 1995). All effects were treated as fixed since genotypes were not sampled randomly but drawn from specific, previously studied populations (see Sultan et al. 2009).

Seed provisioning and germination.—The effect of parental treatment (Par Treat) on mean single achene mass was analyzed using a paired *t* test by genotype (Gen). The effects of Gen, Par Treat, and their interaction on (binomially distributed) percentages of emergence (Expt. 1) and germination (Expt. 2) were analyzed using binary logistic regression with likelihood ratio tests.

For Expt. 2, the effects on seed provisioning of Gen, Treat, and their interaction were analyzed using Type III analysis of variance (ANOVA). The significant Gen × Treat effect was followed by simple effects tests of Treat within each Gen. Survival analysis was used to analyze germination timing because it can account for interval-censoring, right-censoring (some achenes did not germinate by the study's end), and a right-skewed distribution (McNair et al. 2012). A non-parametric hazard model was built using the expectation-maximization iterative convex minorant (EMICM) algorithm (Wellner and Zhan 1997) and significance of Par Treat in each germination treatment (Germ Treat) was assessed with log-rank tests (Fay 1999). Semiparametric proportional hazard regression models with midpoint imputation of intervals were also used to allow for continuous covariates (Cox 1972). The effects of Gen, Par Treat, Germ Treat, and their two- and three-way interactions, both with and without seed provisioning as a covariate, were analyzed and significance assessed with Wald tests. Achene mass was used to estimate seed provisioning for ungerminated (right-censored) achenes (Pearson's $r = 0.94$). The effects on initial germinant mass of Gen, Par Treat, Offspring Treatment (Off Treat), their 2-way and 3-way interactions were analyzed with Type III ANOVA. Analysis of covariance (ANCOVA) was used to test the effect of seed provisioning as a covariate.

Offspring developmental traits.—Par Treat, Off Treat, and Gen main and interaction effects on canopy area, plant height, and leaf number over time were analyzed using repeated-measures multivariate ANOVA (MANOVA) with the Wilks' lambda test statistic following a significant Mauchly's sphericity χ^2 test (Scheiner and Gurevitch 2001). This method uses listwise deletion, so Expt. 1 Offspring Comp was analyzed separately from Offspring Solo and included only two or three time points for leaf number and height, respectively. Percent biomass allocation to root, stem, and leaf tissues in Expt. 1 and to root and shoot tissues in Expt. 2 was analyzed using Wilks' lambda MANOVAs in each Off Treat. Following a significant effect of Par Treat in the multivariate test, univariate tests were conducted to identify tissue-specific effects.

For offspring traits measured at harvest, the effects of Gen, Par Treat, Off Treat, their two-way and three-way interactions, Block (nested within Off Treat in Expt. 1), and Day of Transplant (in Expt. 2) were analyzed using Type III ANOVA. All traits except SLA were Box-Cox transformed to meet ANOVA assumptions. Effect sizes were calculated as partial eta-squared (η_p^2; Lakens 2013). To resolve any context-dependent effects of Par Treat and Gen, similar analyses were conducted within each Off Treat and the mean percent change due to parental competition was calculated for each trait.

RESULTS

Experiment 1: Transgenerational effects of parental competition in moist soil on offspring development

Parental competition significantly altered multiple offspring traits measured during development (Fig. 2; Appendix S1: Table S1) and at harvest (Fig. 3, Table 1), but this parental effect differed in magnitude depending on the offspring treatment. When growing in Competition, progeny of parental competition plants produced greater shoot mass (+34%; Fig. 3a) and allocated more

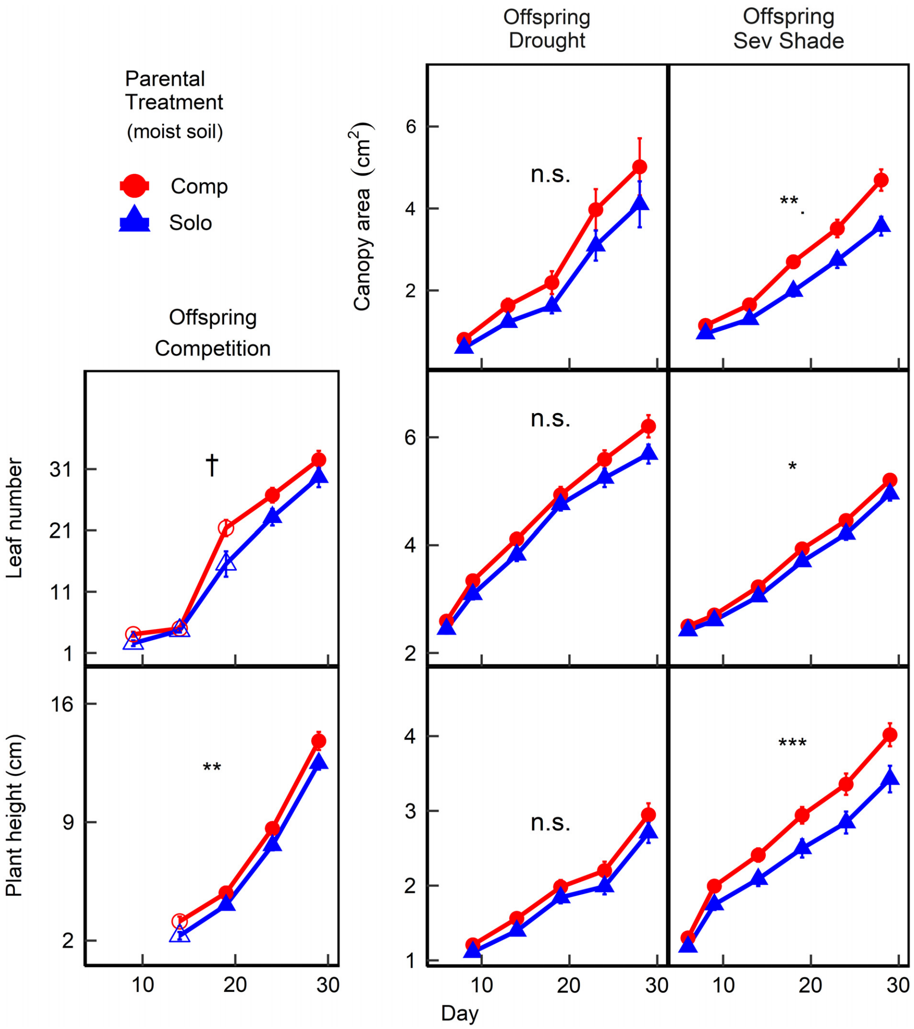

FIG. 2. Effects of parental competition in moist soil on offspring trait expression over time in three contrasting treatments (Experiment 1). Means ± SE (pooled among six genotypes) are shown. *Y*-axes are scaled to the middle 80% of data for each trait (note distinct scales for Offspring Competition treatment). Asterisks indicate significance of parental treatment on offspring in each treatment (n.s. $P \geq 0.10$; † $P < 0.10$; * $P < 0.05$, ** $P < 0.01$; *** $P < 0.001$). Open symbols are used for time points that include only one of two temporal Offspring Competition blocks (details in *Methods*).

of their biomass to stem (+6%) and less to leaf tissues (−5%; Fig. 3b) than progeny of isogenic replicate parents grown without competition. Compared with Parent Solo progeny, Parent Comp progeny also grew taller (+14%) and produced more shoot mass relative to their within-pot (Parent Solo) competitors (+47%). In severe shade, progeny of Parent Comp grew taller (+17%), produced greater total biomass (+23%), allocated more of their biomass to stem (+7%) but less to root tissue (−18%; Fig. 3b), and produced greater total leaf area (+22%) and canopy area (+31%; Fig. 3a) than offspring of Parent Solo plants. The significant Par Treat effects on canopy area, plant height, and leaf number were generally consistent over developmental time (n.s. Par Treat × Time interaction terms, Appendix S1: Table S1). However, for offspring in severe shade, the effect of Par Treat on canopy area became greater in magnitude and more significant over time ($P = 0.003$; +21% at first time point to +31% at last time point; Fig. 2). In contrast, parental treatment had no significant effect on developmental traits ($0.223 < P < 0.848$) or percent biomass allocation ($P = 0.572$) for offspring grown in drought (Fig. 3).

The very large effects of Offspring Treatment across traits (Figs. 2, 3, Table 1) reflect within-generation plasticity in response to the dramatically different offspring conditions chosen to test for context-specific expression. In most traits, the effects of both parent and offspring treatments differed among genotypes (sig. Par Treat × Gen and Off Treat × Gen terms, Table 1). For some traits, expression of genotype-specific parental environment effects varied depending on the immediate

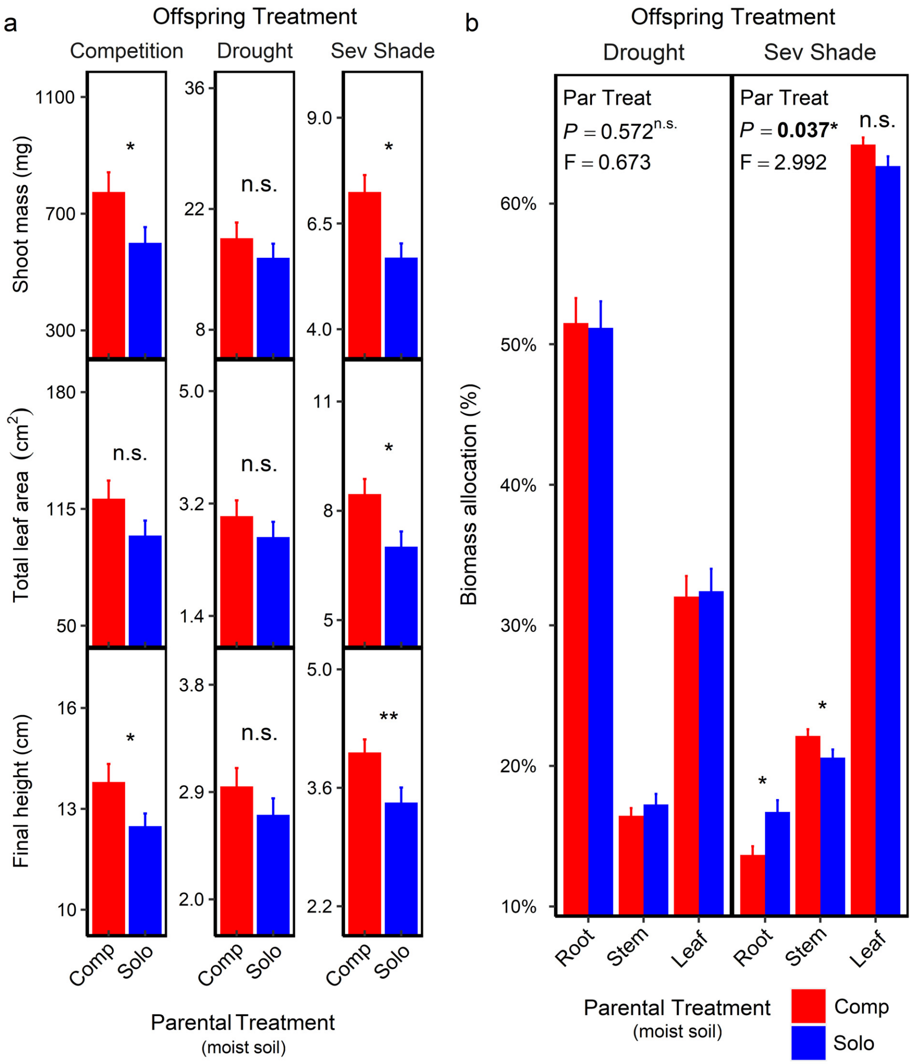

FIG. 3. Effects of parental competition in moist soil on offspring trait expression measured at harvest (Experiment 1). Means ± SE (pooled among six genotypes) are shown; *Y*-axes are scaled to middle 80% of data for each trait and offspring treatment. Asterisks indicate significance of parental treatment on offspring in each treatment (n.s. $P \geq 0.10$; * $P < 0.05$; ** $P < 0.01$). (a) Effects of Parental Competition on offspring shoot mass, total leaf area, and final height in three contrasting offspring treatments. (b) Effects of Parental Competition on percent biomass allocation to leaf, root, and stem tissues in two contrasting offspring treatments (due to no root data in Offspring Competition). Bars sum to 100% but are shown unstacked to display error bars. Following a significant MANOVA effect of parental treatment, ANOVAs were conducted for each tissue type separately; significance of parental treatment is shown.

environmental context (sig. three-way Gen × Par Treat × Off Treat interactions, Table 1).

Experiment 2: Transgenerational effects of parental competition in dry soil on offspring development

Parental competition in dry soil resulted in small, marginally significant negative effects on offspring traits ($0.025 < P < 0.040$), reducing total biomass, mean single leaf area, total root length, and final canopy area (Fig. 4; Appendix S1: Table S3) by 11–14% for offspring growing in both competitive and non-competitive dry-soil conditions. The effects of parental competition in dry soil on canopy area and plant height over time were similarly small but were marginally non-significant (−14%, $P = 0.07$ and −5%, $P = 0.08$; Appendix S1: Table S4). The inherited effects of Parent Comp in dry soil were not significantly differently expressed in the two offspring treatments (n.s. Par Treat × Off Treat interaction term, $P > 0.10$, Appendix S1: Table S3; confirmed by exploratory two-way ANOVAs in each offspring treatment). However, offspring showed significant within-generation plasticity to competition across traits (Off Treat effect: $P < 0.001$, Fig. 4; Appendix S1: Table S3).

TABLE 1. Effects of parental competition in moist soil (Experiment 1).

		Shoot biomass		Specif. leaf area		Total leaf area		Final height		Final leaf no.	
		$R^2 = 0.94$		$R^2 = 0.98$		$R^2 = 0.91$		$R^2 = 0.93$		$R^2 = 0.90$	
Source of variation	DF	P	η_p^2	P	η_p^2	P	η_p^2	P	η_p^2	P	η_p^2
Parent treatment (Par Treat)	1	**0.001****	0.055	0.369	0.004	**0.001****	0.053	**<0.001*****	0.098	**0.001****	0.056
Offspring treatment (Off Treat)	2	**<0.001*****	0.949	**<0.001*****	0.981	**<0.001*****	0.927	**<0.001*****	0.941	**<0.001*****	0.919
Genotype (Gen)	4	**<0.001*****	0.112	**<0.001*****	0.112	**<0.001*****	0.135	**<0.001*****	0.238	**0.005****	0.075
Par Treat × Off Treat	2	0.191	0.017	0.228	0.015	0.236	0.015	**0.030***	0.036	0.411	0.009
Gen × Par Treat	4	**0.030***	0.054	0.456	0.019	0.083†	0.042	**0.007****	0.071	0.320	0.024
Gen × Off Treat	8	**0.016***	0.092	**<0.001*****	0.170	0.187	0.057	**<0.001*****	0.146	**0.008****	0.102
Gen × Par Treat × Off Treat	8	**0.040***	0.080	**0.001****	0.127	0.130	0.063	**0.004****	0.110	0.149	0.060
Block [Off Treat]	24	**0.001****	0.222	**<0.001*****	0.448	0.057†	0.163	**<0.001*****	0.337	0.199	0.136

Notes: Effects of Parental Treatment (Competition vs. Solo), Offspring Treatment (Severe Shade vs. Drought vs. Competition), Genotype, and all two- and three-way interactions on offspring traits at harvest (day 31), based on ANOVA (details in *Methods*). Error DF were 190 or 191, depending on the trait. Adjusted R^2 are shown. η_p^2, partial eta-squared.

Significant P-values are in bold († $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Both experiments: Transgenerational effects of parental competition on seed traits

When parent plants competed in moist soil (Expt. 1), on average, their achenes were 8% smaller by mass ($P = 0.024$), but 20% more likely to emerge as seedlings ($P = 0.034$, Appendix S1: Table S2) than achenes produced by Solo-grown parents.

In contrast, parental competition in dry soil (Expt. 2) did not significantly affect mean individual achene mass ($P = 0.61$) or seed provisioning ($P = 0.763$) compared with achenes produced by Solo parents, although genotypes differed in their seed provisioning response ($P = 0.008$). One genotype (DFF7) produced fewer achenes of larger mass in the Parental Solo treatment, but more achenes of smaller mass in the parental competitive treatment. On average, Parent Comp achenes had a slightly smaller chance of germinating (−3.5%, $P < 0.001$; Appendix S1: Table S2), but note that the large sample size (N = 5,080) means that even small effects can be significant.

When measured 7 d after sowing (26–128 h after germination), germinant progeny of parents competing in dry soil were 28% smaller when grown in the Shade treatment than those of Solo parents ($P < 0.001$; Appendix S1: Table S5; Fig. 5). Although seed provisioning was significantly positively associated with initial germinant mass ($P < 0.001$), accounting for seed provisioning by including it as a covariate increased the effect size and significance of the parental treatment on initial germinant mass (Par Treat effect without covariate: $P = 0.010$, $\eta_p^2 = 0.071$; with covariate: $P < 0.001$, $\eta_p^2 = 0.136$), indicating that parental competition has an effect on initial germinant mass apart from provisioning.

Based on a subsample of 240 individually tracked achenes there was a marginally non-significant trend for Parent Comp achenes to germinate earlier in both Full Light and Shade treatments (Par Treat effect on germination rate: $P = 0.063$); after accounting for seed provisioning as a covariate in the model, the effect of Par Treat on germination rate was significant ($P = 0.021$; Appendix S1: Table S5). Although the Par Treat × Off Treat interaction term was not significant ($P = 0.317$; Appendix S1: Table S5), analyses within each germination treatment revealed that although the trend was consistent in both germination treatments, Parent Comp achenes germinated significantly faster than Parent Solo achenes only in Full Light conditions (median = −20 h, $P = 0.013$; Appendix S1: Fig. S4).

DISCUSSION

Parental competition can induce significant transgenerational effects on offspring phenotypes that persist to early adulthood

While transgenerational effects of herbivory have been well documented (reviewed by Holeski et al. 2012), little information is known about inherited developmental effects of other biotic factors. In two experiments with different soil moisture levels, we used naturally evolved lines of the well studied plant *P. persicaria* to compare isogenic offspring that differed only in the competitive density of their parents. Overall we found that, as with abiotic plant stresses in various taxa such as shade, drought, and temperature (Galloway and Etterson 2009, Sultan et al. 2009, Whittle et al. 2009), parental intraspecific competition-induced significant effects on offspring growth, morphology, and life-history. Moreover, the biotic stress of competition imposed transgenerational effects on *P. persicaria* offspring phenotypes that were distinct from the known inherited effects of its

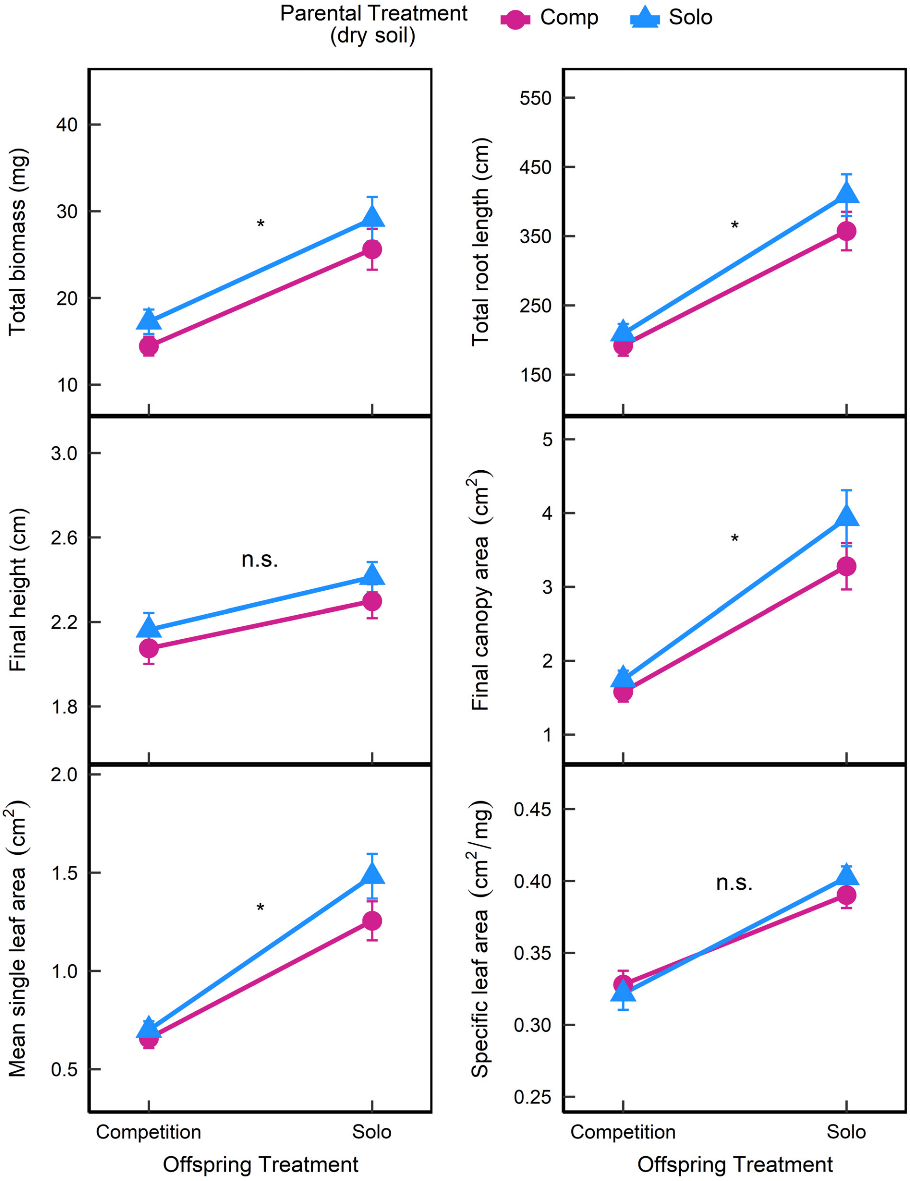

FIG. 4. Effects of parental competition in dry soil on offspring trait expression measured at harvest in two offspring treatments, Competition and Solo, both in dry soil (Experiment 2). Means ± SE (pooled among six genotypes) are shown. *Y*-axes are scaled to the middle 80% of data for each trait. Significance of parental treatment across both offspring treatments is indicated (n.s. $P \geq 0.10$; * $P < 0.05$).

component abiotic stresses: drought, shade, and nutrient deprivation (Sultan 1996, Herman et al. 2012, Baker et al. 2018, 2019). Although studies of other taxa are needed to determine their prevalence, such effects may be particularly important in herbaceous plant communities, which are frequently characterized by intense competition (Turnbull et al. 2004, Bonser and Ladd 2011).

By demonstrating substantial, specific developmental effects of parental competition, our results provide new insight into transgenerational sources of variation in plant populations. As discussed below, these effects varied depending on the particular parental and offspring growth environments. Existing studies testing parental effects of competition have primarily focused on seed traits: parent plants grown in competitive vs. noncompetitive environments produced seeds with smaller mass in *Raphanus sativus*, *Nemophila menziesii*, and *Brassica rapa* (Mazer and Wolfe 1992, Platenkamp and Shaw 1993, Dechaine et al. 2015) and increased percent germination in *Arabidopsis thaliana* (Leverett et al. 2018), while at constant competitive density the frequency or identity of conspecifics has also been shown

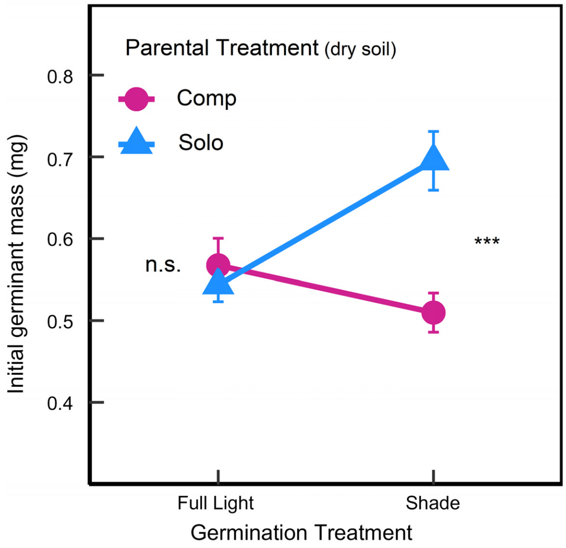

FIG. 5. Effects of parental competition in dry soil on the initial mass (7 d after sowing) of individually tracked germinants in the growth chamber (Experiment 2, Seed Traits). Means ± SE (pooled among six genotypes) are shown. *Y*-axis is scaled to the middle 80% of data. Asterisks indicate significance of parental treatment on offspring in each treatment (n.s. $P \geq 0.10$; *** $P < 0.001$).

to influence these seed traits (Bhaskar and Vyas 1988, Violle et al. 2009, Walter et al. 2016, Germain et al. 2019). Dechaine et al. (2015) tested for parent-competition effects beyond the seed stage using recombinant inbred lines of *B. rapa* derived by crossing two artificially selected (rapid-cycling and seed oil) genotypes. They found a genetically variable effect of maternal competitive environment on offspring phenotypes but no main effect; however, this result may not be applicable to systems that evolved under natural selection. Indeed, the one prior study testing for transgenerational effects of parental competition on offspring phenotypes in a naturally evolved system, the apomict *Taraxacum brevicorniculatum*, found a significant main effect of the parental competitive environment on offspring growth rate, SLA, root mass, root carbohydrate storage, and plant height (Puy et al. 2021). The authors propose that such effects comprise a resource-conservative strategy that is putatively adaptive for perennial plants facing intense competition. Because *P. persicaria* is an annual plant, the expected adaptive response would instead be to maximize rather than conserve resources in the face of competition. Although the specific developmental effects of parental competition in the two studies differed, yet both studies provide support for adaptive transgenerational effects of plant-plant competition (see "Transgenerational effects on offspring development varied depending on parental and offspring growth environments").

Interestingly, offspring developmental trajectories for height, leaf number, and canopy area showed that transgenerational effects of parental competition either persisted or increased as plants grew. Based on theory, parental effects are often predicted to be greater early in development, before offspring can accurately sense and respond to their own environment, and then to diminish (Uller 2008, Auge et al. 2017); this prediction is empirically supported by a number of studies in both plants (Roach and Wulff 1987, Weiner et al. 1997, Wadgymar et al. 2018) and animals (Rotem et al. 2003, Shama et al. 2014). However, because an initial growth difference may be amplified over the life cycle (Stanton 1984, Metz et al. 2010), other studies confirm our finding that transgenerational effects may have a consistent or increasing impact as progeny develop (in plants: Case et al. 1996, Sultan et al. 2009, Baker et al. 2019; in animals: Champagne and Meaney 2006, Onyango et al. 2008).

Our data also provide evidence for genotype-specific responses to parental competition. In some cases, *Polygonum* genotypes differed in their responses to a particular combination of parental and immediate environments. Such *genotype-by-parental environment* and *genotype-by-parental environment-by-offspring environment* interactions have been found in numerous plant and animal studies (reviewed by Marais et al. 2013, Plaistow et al. 2015, Vu et al. 2015, Herman and Sultan 2016), and may be a general feature of transgenerational environmental effects. Importantly, this kind of genetic variation provides the potential for populations to evolve altered patterns of transgenerational plasticity (Day and Bonduriansky 2011, Uller 2012, Herman et al. 2014, Sultan 2017, Alvarez et al. 2020). We note that our proof-of-concept study included a limited sample of genotypes; future experiments using broader sampling would be needed to robustly characterize these effects at the population or species level.

Transgenerational effects of parental competition were not explained by seed provisioning

If the transgenerational effects of parental competition reflected simple increases or decreases in the amount of resources provisioned to seeds, we would expect to find correlated overall effects on offspring growth that were consistently positive or negative, respectively, across the different offspring treatments. While parental competition in moist soil resulted in smaller (lower mass) achenes, many of the subsequent seedling developmental effects were significantly positive, refuting the expectation that positive transgenerational effects will be mediated through increased offspring provisioning (i.e., "silver-spoon effect" Grafen 1988). Effects on provisioning and on offspring growth were also decoupled for parental competition in dry soil which, perhaps surprisingly, caused no reduction in either achene or seed mass. Yet despite their equivalent seed mass, these offspring did show overall negative growth effects compared with progeny of parents grown singly in dry soil, starting with significantly lower mass as initial germinants. This negative effect remained even after accounting for seed provisioning as a covariate.

Results of both parental competition experiments suggest that the effects of parental environment on seed mass may be a limited indicator to researchers of subsequent developmental impacts. This decoupling in part reflects the fact that seed mass does not capture environmentally-sensitive qualitative aspects of offspring provisioning such as macronutrient concentration (Roach and Wulff 1987, Herman and Sultan 2011). Despite holding constant the total quantity of seed provisions, *Polygonum* plants competing in dry soil may have decreased specific aspects of seed nutrient content as a result of their own nutrient stress (see Parrish and Bazzaz 1985, Hara and Toriyama 1998, Tungate et al. 2002), causing reduced progeny growth. Consistent with this hypothesis, these parental competition achenes were slightly less likely to germinate than achenes of singly grown parents; testing the proportion of ungerminated seeds that were nonviable vs. dormant would be necessary to confirm that lower germination propensity reflected lower quality (Violle et al. 2009, Baskin and Baskin 2014). In this experiment, we measured both germination timing and the initial mass of germinants (7 days after sowing), an indicator of the joint consequences of seed quality and germination timing (after accounting for seed mass as a covariate). Parental competition in dry soil resulted in significantly lower germinant mass, but only for offspring germinating in shade. This result is consistent with the view that this parental treatment led to offspring of lower quality: since offspring of drought-stressed competing and non-competing parents germinated at the same time in shade, any differences in seed quality could have led to a greater growth differential as of the early germinant timepoint. In contrast, when the two sets of progeny were germinated in full sun, the offspring of dry soil, solo-grown parents germinated 29% later (based on medians), so their germinant mass as of day 7 was not significantly greater.

Parental conditions may also influence offspring development through changes to seed-borne signaling factors such as hormones, non-coding RNAs, and epigenetic marks, none of which are reflected in the mass of seed reserves. As these inherited, environmentally induced factors can result in context- and trait-specific effects on phenotypic expression (reviewed by Hauser et al. 2011, Blake and Watson 2016), it seems plausible that they may have contributed to the developmental effects of parental competition in moist soil (next section). In particular, DNA methylation is a well known mediator of inherited environmental effects in plant systems (Verhoeven et al. 2010, Dowen et al. 2012, Zheng et al. 2013) that has previously been found to play a role in mediating the specific, functionally adaptive transgenerational effects of both parental drought and shade on offspring development in *P. persicaria* (Herman and Sultan 2016, Baker et al. 2018). Conversely, the overall slightly negative effects of Parental Competition vs. Parental Solo in dry soil seem unlikely to result from a particular, competition-induced epigenetic modification. Although environmentally induced epigenetic changes of consistently negative effect appear to mediate several mammalian diseases (Skinner et al. 2010, Cavalli and Heard 2019), they appear to be rare in plants (i.e., they have been implicated only in responses to parental radiation [Boratyński et al. 2016] and herbicides [Baucom et al. 2008]). Future studies testing inherited effects of parental competition on epigenomic variation in *Polygonum* would provide further insight into the precise transgenerational mechanisms driving the phenotypic changes found in this study.

Transgenerational effects on offspring development varied depending on parental and offspring growth environments

The developmental effects of parental competition in moist soil on *P. persicaria* offspring were magnified (and only significant) when offspring were growing in similarly moist and light-limited conditions (i.e., either aboveground competition or severe shade simulating a dense canopy, rather than sunny and dry). Compared with offspring of isogenic parent plants that were grown singly, the offspring of competing parents in these light-limited treatments allocated more tissue to shoots, grew taller, and produced more leaves per unit time, resulting in greater total leaf area and biomass at harvest. These phenotypes are associated with increased competitive success and lifetime fitness in light-limited environments (Galloway and Etterson 2009, Baker et al. 2019). This suggests that neighbor shading cues detected by competing parents led to ‘anticipatory’ effects in that they enhanced the adaptive developmental response of offspring encountering light limits, whether from neighbors or a dense canopy.

Interestingly, comparing these results with a prior study in *P. persicaria* suggests the possibility of even more precise transgenerational effects. In that study (Baker et al. 2019), simulated parental canopy shade conferred a greater growth advantage on offspring grown in simulated severe canopy shade than on those grown with neighbor competition; yet in the present case, parental competition effects were greater for offspring in competition than those in severe shade. Such precise parental signaling is plausible: although both experimental neighbor and canopy shade reduce photosynthetically active radiation (PAR) and R:FR spectral ratio (*Methods*; see Roig-Villanova and Martínez-García 2016), plants in competition may more specifically detect neighbors via root exudates, localized nutrient depletion zones, volatile organic compounds, and physical contact (Gruntman and Novoplansky 2004, Pierik et al. 2013).

The evolution in this system of adaptive transgenerational effects of moist-soil parental competition is consistent with theoretical expectations. Adaptive transgenerational plasticity is favored in environments that are both variable and at least moderately correlated across generations (Kuijper et al. 2014, Uller et al. 2015, Colicchio and Herman 2020). Aboveground competitive conditions in *P. persicaria* populations meet these expectations: although neighbor density varies within sites and across seasons, there is a broad correspondence in the proportion of light intercepted by neighbors from year to year at the scale of individual microsites (Pearson correlation = 0.57, based on 21 multipoint microsite averages taken across the growth season at each of four field populations in 2019 and again in 2020, R. Waterman and C. Babbin, *unpublished data*). As the species is also gravity dispersed, with 95% of achenes falling within 1 m^2 of the parental plant axis (R. Waterman, *unpublished data*), offspring are likely to encounter microsites resembling those of their parents. In such conditions, anticipatory transgenerational effects can increase offspring fitness by eliminating the time lag between perceiving and responding to immediate environmental cues (Uller 2008, Bonduriansky and Day 2009). Furthermore, when environments predictably change across the growth season, the environment experienced by the parent at reproductive maturity may be a more accurate predictor of the progeny's future selective environment than the progeny's own early developmental conditions (Crone 1997, Auge et al. 2017). Accordingly, the evolution of adaptive transgenerational effects may be favored in annual plant communities where intense neighbor competition during seed production is a good indicator that offspring will face a similarly competitive environment, even though seeds often germinate when surrounding vegetation is sparse (Leverett et al. 2016). Consistent with this point, the intensity of aboveground competition (% light intercepted by neighboring vegetation) in field populations of *P. persicaria* dramatically increases from early to late growing season (R. Waterman, *unpublished data*).

In contrast with the variable, putatively adaptive transgenerational effects of competition found in the first experiment, the developmental impact of parental competition in the follow-up experiment was not consistent with an adaptive match. When parents competed for limited water, their offspring showed slightly *reduced* overall growth in similarly dry conditions, whether grown alone or with competitors (marginally significant decreases in total root length, total canopy and mean single leaf area, canopy area, and total biomass; nonsignificant decrease in height). Surprisingly, these small, consistently negative effects were not associated with a lower quantity of seed provisioning, but rather appear to have been mediated by changes in provision quality (see previous section).

Although comparing the results of the two experiments points to intriguing hypotheses, this comparison must be made with caution. In addition to the change from moist to dry parental soil, the experiments were carried out at different times and in different offspring conditions (including pot size, measurement period, and light intensity in the growth chamber vs. the greenhouse; see *Methods*). We note however that in previous studies, parental drought (Sultan et al. 2009, Herman et al. 2012, Herman and Sultan 2016) and shade (Baker et al. 2018) resulted in similar adaptive developmental effects on offspring when grown in the greenhouse in summer or in the growth chamber in winter (in smaller pots). Specifically, because the above-cited papers confirmed growth advantages including greater root length in chamber-grown offspring of drought-stressed parents, the absence of such effects for offspring of parents under exacerbated drought stress due to competition seem unlikely to be explained by this experimental venue.

Rather, it is also possible that the distinct effects of parental competition in the two experiments may reflect how soil conditions shape competitive stress and therefore its transgenerational impact. Densely spaced parent plants in moist, nutrient-rich soil compete primarily for light, but when soil is kept dry, parents compete for moisture and nutrients as well, since dry soil limits nutrient availability and uptake (Fitter and Hay 1987, He and Dijkstra 2014, Bista et al. 2018). In the present study, the dry vs. moist soil environment of competing parents may have caused these very different effects on progeny development in two (non-mutually exclusive) ways. First, the more broadly resource-limited parental plants competing in dry soil may have reduced the quality of provisioning to their offspring, leading to the observed reductions in overall progeny growth. Parental resource limits are a well known cause of reduced provisioning quantity and/or quality and subsequent seedling growth in numerous plant taxa (reviewed by Roach and Wulff 1987, Fenner and Thompson 2005*a*).

Second, the different, concurrent resource stresses imposed by competition in dry soil may have led to opposing transgenerational influences. In this species, individual abiotic stresses in the parental generation cause specific, contrasting effects on offspring. Parental drought leads to greater seed mass, root allocation, and root extension rate in offspring, resulting in higher survivorship in dry soil than progeny of moist-grown parents, while parental shade results in unchanged or slightly lower seed mass but increased offspring shoot biomass allocation, specific and total leaf area, and competitive performance in shade (Sultan 1996, 2001, Herman et al. 2012). These adaptive transgenerational effects of both drought and shade for offspring in similar conditions are accompanied (and potentially mediated) by DNA methylation (Herman et al. 2012, Baker et al. 2018). The specific effects of parental nutrient limitation include reduced seed mass and overall seedling growth despite increased root allocation (Sultan 1996, 2001); their transmission mode has not been studied. In the present study, intense aboveground competition in moist soil may have allowed for the transmission of a dominant neighbor-shade signal from parents to offspring. However, the simultaneous light, water, and nutrient stresses faced by plants competing in dry soil may have induced opposing signals with respect to provisioning and development, resulting in little net effect beyond a slightly negative overall effect on offspring growth traits, likely due to the negative impact of parental nutrient limitation. Further studies in *Polygonum* that test for possible transmission mechanisms may resolve whether this slightly negative impact reflects distinct epigenetic signals, an overall change in seed composition, or a combination of the two transmission modes (Adrian-Kalchhauser et al. 2020). Studies in other systems indirectly support the hypothesis that multiple stresses may induce opposing progeny responses by showing either contrasting effects of different parental stresses on progeny phenotypes (Verhoeven and van Gurp 2012, Suter and Widmer 2013, Sandner et al. 2018), or a neutral or negative main effect of a complex field-induced parental stress (Schmitt et al. 1992, Hereford and Moriuchi 2005, Pías et al. 2010). Indeed, the possibility of complex, opposing developmental signals may help explain why experimentally induced transgenerational effects often appear to be unexpectedly subtle or absent (Uller et al. 2013). To clarify the precise transgenerational effects of aboveground and belowground competition, future experiments might employ physical apparatuses to directly manipulate root and shoot competition (reviewed by Kiær et al. 2013) or factorially vary individual resource levels in the parental generation.

Conclusions

This study shows for the first time that intraspecific competition can induce transgenerational effects on offspring phenotypes. It does so in ways that depend on growth conditions in both parent and offspring generations. Parental competition under ample soil resource conditions conferred a growth advantage that was most pronounced on offspring in similarly light-limited environments (i.e., either neighbor or simulated canopy shade). In a follow-up experiment, parental competition under limited soil resources led to slight but consistently negative offspring growth effects. Importantly for experimental design, these complex transgenerational effects on offspring development are not predicted by individual seed mass, but may instead be mediated by changes to seed nutrients and molecular signaling factors. Further research including field studies will illuminate the potential role of transgenerational effects of competition in natural populations, where a multitude of covarying abiotic factors and ecological interactions are at play.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3531/suppinfo

OPEN RESEARCH

Data (Waterman and Sultan 2021) are available on Figshare: https://doi.org/10.6084/m9.figshare.14109713.