

POPULATION DIFFERENTIATION AND PLASTICITY IN VEGETATIVE ONTOGENY: EFFECTS ON LIFE-HISTORY EXPRESSION IN *ERYSIMUM CAPITATUM* (BRASSICACEAE)¹

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- **Premise of the study:** Distinguishing the contributions of phenotypic plasticity vs. population differentiation to variation in the life history of plants throughout their range is important for predicting their performance after dispersal or their responses to environmental change. In *Erysimum capitatum*, plants in alpine environments are iteroparous perennials, but those below tree line are semelparous perennials. We tested population differentiation and plasticity of life-history variation and explored the effects of plastic responses at the prereproductive stage on life-history expression.
- **Methods:** Plants from alpine and below tree-line populations were grown in a common greenhouse environment. Soil water content at the prereproductive stage was manipulated to simulate field condition. Because rosette ontogeny of *E. capitatum* (i.e., production of multiple rosettes, reproductive allocation, and degeneration of rosettes) was highly associated with in situ life-history variation, water effects on rosette ontogeny and life history were assessed.
- **Key results:** Plants from alpine populations showed higher postreproductive survival than those from low-elevation populations in the greenhouse environment, and such difference can be explained by differential rosette ontogeny at both the prereproductive and reproductive stage. In addition, rosette development at the reproductive stage was plastic to water availability at the prereproductive stage, which influences life-history expression as adults.
- **Conclusions:** Because water availability is lower at low-elevation sites, in situ population differentiation is likely caused by plasticity to water availability as well as by genetic differentiation or maternal effects. Plastic or evolutionary changes of pre-reproductive traits are expected to influence adult life-history expression, which possibly influence population demography.

Key words: altitudinal variation; developmental stage; *Erysimum capitatum*; life-history strategy; phenotypic plasticity; population differentiation.

Geographic variation in ecologically important traits is attributable both to genetic differentiation and phenotypic plasticity (Claussen et al., 1940; Endler, 1977; Sultan, 1987; Linhart and Grant, 1996; Geber and Griffen, 2003). Patterns of genetic differentiation and plasticity influence present and future interactions of organisms with their environments in ways that affect species ranges, invasiveness, and community composition (Kirkpatrick and Barton, 1997; Sakai et al., 2001; Miner et al., 2005; Bridle and Vines, 2007). Thus, characterizing plasticity and genetic differentiation provides critical information for predicting the evolutionary and ecological responses of plants to new environments experienced after dispersal and as a result of anthropogenic climate change (Holt, 1990; Walther, 2003; Jump and Peñuelas, 2005; Parmesan, 2006; Charmantier et al., 2008).

Alpine ecosystems are at the edges of climatic clines, and their geographic ranges are projected to decrease rapidly. Phenotypic plasticity in response to climatic variation may criti-

cally affect the persistence of alpine plant populations (Theurillat and Guisan, 2001; Diaz and Eischeid, 2007; Parry et al., 2007). In particular, the risk of population extinction may depend on whether plasticity follows a pattern of cogradient variation (Eckhart et al., 2004). Cogradient variation occurs when the plasticity of a trait in response to an environmental gradient is in the same direction as adaptive genetic differentiation (Levins, 1968; Conover and Schultz, 1995). Since climate change causes environments at high altitude to become similar to those at low altitude, if traits of alpine plants become more similar to those of locally adapted low-altitude plants through phenotypic plasticity, such plasticity could improve plant performance in the face of environmental change (Byars et al., 2007; Charmantier et al., 2008). To test for such cogradient variation requires quantifying both genetic differentiation and plasticity to relevant environmental factors (Conover and Schultz, 1995).

An important predicted outcome of climate change is altered availability of water. Higher temperature alters the timing of snowmelt at high altitude. Earlier snowmelt and therefore longer growing seasons could increase the evaporation and transpiration of soil water, causing drier soils during the summer growing season (Taylor and Seastedt, 1994; Harte et al., 1995; Calanca, 2007; Lambrecht et al., 2007). Because soil water content is positively correlated with altitude in many temperate mountains, climate change could cause a novel drought stress for plants at higher altitudes (Körner, 2003; Parry et al., 2007). Evaluation of plasticity of alpine plants to soil water availability is therefore relevant for predicting how climate change may affect their phenotypic and life-history expression and fitness (Harte et al., 1995).

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Western wallflower (*Erysimum capitatum*, Brassicaceae) is a rosette plant with a broad altitudinal distribution in the Colorado Rocky Mountains, from below tree line to alpine tundra (Price, 1987). It exhibits natural variation in life history, morphology, and demography across altitude (Kim and Donohue, 2011). In particular, iteroparity (polycarpy) is prevalent in alpine populations, and semelparity (monocarpy) is prevalent in populations below tree line (Table 1). Populations with semelparity and iteroparity exhibit distinct demography; compared with semelparous populations, iteroparous alpine populations have lower projected population growth rates and smaller elasticities of seedling recruitment and a rapid transition to reproduction (Kim and Donohue, 2011). Thus, a change in semelparous/iteroparous life history in response to climate change could significantly affect population demography (Franco and Silvertown, 1996).

It is not known whether such variation in semelparous/iteroparous life history is genetically based or environmentally induced, especially because plant reproductive strategies are notoriously plastic to diverse environmental factors, including nutrient availability, light quality and abundance, successional stage of the habitats, and pollinator abundance (Van Baalen and Prins, 1983; Verkaar and Schenkeveld, 1984; Paige and Whitham, 1987). In particular, soil water content in low-elevation semelparous populations in *E. capitatum* is significantly lower during the growing season compared with that in alpine iteroparous populations, as graphed in Appendix S1 (see Supplemental Data with the online version of this article), and vegetative plants in semelparous low-elevation populations had high mortality during the summer (Kim and Donohue, 2011). In contrast, no indication of drought stress was found in iteroparous alpine populations, so natural variation in semelparous/iteroparous life history in *E. capitatum* might be simply due to drought-induced mortality of reproductive plants in low-elevation populations. We conducted a common garden experiment with benign water conditions to determine whether natural variation is imposed by extrinsic factors or by intrinsic physiological mechanisms.

Alternatively, if the production of multiple rosettes at the prereproductive stage is a key developmental prerequisite of iteroparity, as observed in the field (Kim and Donohue, 2011), in situ variation in life-history strategy might be induced by differential production of rosettes. Thus, it is necessary to test whether the observed variation in prereproductive rosette production and its association with iteroparity is genetically based or environmentally induced. Because the production of vegetative shoots is highly plastic to soil water availability in several plant species (Rochow, 1970; McIntyre, 1977; Körner, 2003),

and since soil water content differs between semelparous and iteroparous populations, we manipulated soil water availability at the prereproductive stage to determine phenotypic plasticity and differentiation of the ontogeny of rosettes, and its effects on the life history.

Specifically, we addressed the following questions: (1) Do populations from different altitudes differ in morphological and developmental traits as well as iteroparity when plants are grown in a common environment with ample soil water content? (2) Are traits plastic to soil water content experienced during the prereproductive stage in a manner that is consistent with cogradient variation? (3) How do developmental traits interact to determine iteroparity, and do these interactions differ across altitude?

MATERIALS AND METHODS

Study populations—Seeds were collected from six populations of *Erysimum capitatum* in the Colorado Rocky Mountains in 2005. In each of three watersheds, one population was chosen from alpine tundra sites (H1, H2, and H3), and one population was chosen from below tree line (L1, L2, and L3; Table 1). Plants from alpine tundra sites are referred to as *high-elevation populations* and those from below tree line as *low-elevation populations*. Each watershed is referred to as a *region*. Two alpine populations (H1 and H2) are unambiguously iteroparous, two low-elevation populations (L2 and L3) are semelparous, and one high-elevation population (H3) and one low-elevation population (L1) exhibit an intermediate level of iteroparity (Table 1).

In the field, plants in semelparous populations grew faster and reproduced more quickly than iteroparous populations (Kim and Donohue, 2011). Around 30% of plants in semelparous populations initiated reproduction in their second year, but plants in iteroparous populations were not reproductively mature until the end of their third growing season. The average lifespan of plants in iteroparous populations is not known.

Natural variation in life history is strongly associated with rosette ontogeny. *Erysimum capitatum* is acclonal, but an individual plant can bear multiple basal rosettes (Price, 1987; Rollins, 1993). Within a season, a rosette may or may not produce an inflorescence from its terminal apical bud. Hereafter, a rosette with an inflorescence is referred to as a *reproductive rosette*, and a rosette without an inflorescence is referred to as a *vegetative rosette*. The leaves of reproductive rosettes degenerate during the reproductive period, but those of vegetative rosettes remain alive and photosynthetic throughout the year (Kim, personal observation). In alpine iteroparous populations, most reproducing plants have multiple rosettes at the beginning of reproduction and allocate some rosettes to reproduction, but they keep others in the vegetative stage. In contrast, plants in low-elevation, semelparous populations generally have one or two rosettes at the beginning of reproduction, and all rosettes become reproductive. Because the leaves of vegetative rosettes remain alive and photosynthetic throughout the year, rosette production and rosette allocation to reproduction are the determinant factors of the reproductive strategy of *E. capitatum*, as in other rosette species (Verkaar and Schenkeveld, 1984; Young and Augspurger, 1991).

Experimental design—Seeds from 15 field plants (maternal genotypes) of each population were sprinkled into flats filled with commercial soil medium (Metromix 360; Sungro, Bellevue, Washington, USA) and were saturated with water in the Harvard University greenhouse. Seedlings with six leaves were transplanted into 7.6 × 7.6 × 14 cm plastic pots filled with the same soil medium 3 wk later. One seedling per maternal genotype was randomly assigned to one of three water treatments, resulting in a total of 270 plants (six populations × 15 maternal genotypes per population × three water treatments). The pots were randomly positioned on a greenhouse bench (1 × 4 m). All plants were maintained at 17°C with a 12-h photoperiod. Supplemental light from high-intensity mercury halide lights was provided between 6:00 a.m. and 6:00 p.m. if ambient light fell below 760 μmol m⁻² · s⁻¹ for more than 15 min.

We conducted a water manipulation experiment at the prereproductive stage to quantify plasticity to water during the stage at which rosettes are produced. After the seedlings were transplanted, three water levels were imposed on the basis of field measurements of water availability: high (HW), low (LW), and fluctuating (FW) water treatments. In natural populations, soil water content varied from 4% to 32% (v/v) from June to August 2007 (online Appendix S1).

TABLE 1. Source populations of *Erysimum capitatum* in Colorado, USA, with their altitude and life history observed in situ.

Region	Population	Altitude (m a.s.l.)	Survival rate of reproducing plants (%)	Life history
1 (Gunnison County)	H1	3191	86.92 (2.44)	Iteroparous
	L1	2630	17.00 (9.35)	Intermediate
2 (Clear Creek County)	H2	3636	71.75 (11.73)	Iteroparous
	L2	2234	0.00 (0.00)	Semelparous
3 (Boulder County)	H3	3505	20.05 (9.35)	Intermediate
	L3	1831	3.45 (3.45)	Semelparous

Survival rate of reproducing plants was measured in six natural populations from 2004 to 2007, and the average (SE) of survival rate is given.

Soil water content in the L2 and L3 populations was below 10% (v/v) during the growing season in 2007, and more than 90% of seedlings died of drought in the field (Kim and Donohue, 2011). The water content of the LW treatment was maintained at 10–15% to avoid fatal water stress to seedlings, whereas that of the HW treatment was maintained at 20–30% (v/v), and that of the FW treatment varied between 10–30% (v/v). To implement the water treatments, soil was air dried for 10 d, and each pot was filled with the same weight of soil. Volumetric water content (v/v), which was measured in natural populations, was converted into gravimetric water content (m/m) on the basis of soil density (Campbell Scientific, 2001). Preliminary tests showed that soil water content of HW and LW treatments was above the lower limit after 3 d, as was the soil water content of FW after 6 d. Thus, soil water content was monitored by weighing pots every 3 d, and water was added as necessary to achieve the highest water content within each treatment every 3 d for HW and LW treatments and every 6 d for FW treatments.

After growing for 3 mo in the greenhouse in their respective treatments, all plants were transferred to a growth chamber (Harris Environmental Systems, Andover, Massachusetts, USA) and vernalized at 6°C for 5 mo to induce reproduction. Subsequently, all plants were moved to the greenhouse with the same temperature and light conditions that they experienced before vernalization, and 100 mL water was added to each pot in all treatments every week. We imposed benign water conditions at this stage to prevent drought-induced postreproductive mortality so that we could compare postreproductive mortality between high- and low-elevation populations caused by intrinsic senescence. Because the species naturally outcrosses, flowers were randomly out-crossed with plants from the same population. Six plants (two each of H2, H3, and L3 plants) did not bolt after vernalization, and 15 plants (one H1, three H2, five H3, two L3, and four L1 plants) died before they had matured fruits, so they were removed from the analysis of postreproductive survival. This resulted in a total of 249 reproductive plants.

Measurements of plant traits—The key indicator of iteroparity in *E. capitatum* is the number of viable rosettes (rosettes with photosynthetic leaves) at the end of reproduction (Kim and Donohue, 2011). We recorded the number of viable rosettes, and the diameter and number of leaves of all rosettes on each plant, from the prereproductive stage, just before vernalization was imposed, to the end of reproduction. Plants were maintained for 2 mo after the end of reproduction until inflorescence stems and leaves dried. The number of fruits and survival of reproducing plants were recorded at the end of the experiment.

All reproductive rosettes degenerated during the reproductive period. Some nonreproductive vegetative rosettes that were produced at the prereproductive stage also degenerated during the reproductive period. In addition, new vegetative rosettes were produced during the reproductive period, and they did not degenerate but remained viable throughout reproduction. Therefore, the number of viable rosettes at the end of reproduction depends on the ontogeny of rosettes: specifically, how many rosettes that existed at the prereproductive stage became reproductive, how many vegetative rosettes degenerated during the reproductive period, and how many new vegetative rosettes were produced during the reproductive period.

On the basis of the above observations, three traits were used as measurements of rosette ontogeny. First, the proportion of prereproductive rosettes that became reproductive was calculated as the number of reproductive rosettes divided by the number of rosettes that existed just before vernalization. Second, the proportion of vegetative rosettes that degenerated during the reproductive period was calculated as the number of vegetative rosettes that degenerated during the reproductive period divided by the number of vegetative rosettes at the beginning of reproduction. Ten plants did not have any vegetative rosette during reproduction because all rosettes that existed before vernalization became reproductive. The proportion of rosettes that degenerated during the reproductive period of those plants was treated as a missing value. Third, the number of rosettes produced during the reproductive period was recorded. Vegetative rosettes that existed at the prereproductive stage formed elongated visible stems connected to the main axis of a plant. In contrast, vegetative rosettes produced during the reproductive period were at the base or in the middle of inflorescences without visible elongated stems, so they could be distinguished from vegetative rosettes that existed at the prereproductive stage.

Statistical analyses—All statistical analyses used the SAS statistical package version 9.2 (SAS Institute, Cary, North Carolina, USA). To test whether in situ altitudinal variation in life history was manifest in a common greenhouse environment, and to examine phenotypic plasticity of iteroparity in response to the water treatments, analysis of variance was conducted on two key indicators of iteroparity: postreproductive survival of reproductive plants, and the number

of viable vegetative rosettes at the end of reproduction. For postreproductive survival, a logistic model with a binomial error distribution was used, including binary survival (1 for surviving and 0 for dead plants) as a dependent variable and source altitude (high- vs. low-altitude), water treatment, region, altitude \times water interaction, altitude \times region interaction, water \times region interaction, and altitude \times water \times region interaction as independent variables (SAS Proc GENMOD). Region was a fixed factor because it was chosen on the basis of accessibility to study populations and convenience for field study. However, a separate analysis of variance with region as a random factor also was conducted to compare differences between fixed and mixed models. To analyze the number of viable rosettes at the end of reproduction, analysis of variance (SAS Proc GLM) was conducted, with the same independent variables that were used to analyze postreproductive survival.

Analysis of variance (SAS Proc GLM) using the same model as above was conducted to compare morphological and reproductive traits between high- and low-elevation populations across water treatments. Dependent variables included leaf number per rosette before vernalization, maximum diameter of rosettes before vernalization, number of rosettes before vernalization, proportion of rosettes allocated to reproduction, number of reproductive rosettes, proportion of vegetative rosettes that degenerated during the reproductive period, number of vegetative rosettes produced during the reproductive period, and number of fruits per individual. Leaf number per rosette and fruit number were log transformed; the proportion of rosettes allocated to reproduction and the proportion of vegetative rosettes that degenerated during the reproductive period were arcsine square root transformed to satisfy normality assumptions. To interpret altitude \times region, water \times region, or altitude \times water \times region interactions, subanalyses of variance were conducted within each altitude, region, or population.

To determine the effect of morphological traits on life-history expression, a path model was constructed. Because water treatment was applied only at the prereproductive stage in this experiment, it was hypothesized that water treatment influenced prereproductive traits, prereproductive traits affected the production or degeneration of rosettes during the reproductive period, and both prereproductive and reproductive traits, in turn, influenced the number of rosettes at the end of reproduction as well as fruit production. The number of rosettes at the end of reproduction and fruit production, in turn, were hypothesized to affect postreproductive survival. Path coefficients were estimated by using SAS Proc GLM with water treatment and population as covariates to control for possible differences in unmeasured traits. All traits were standardized with zero means and one standard deviation, following Mitchell (2001).

Because path coefficients do not provide information on the overall association of each trait with iteroparity, a simple regression analysis also was conducted on the two key indicators of iteroparity: postreproductive survival (SAS Proc LOGISTIC) and the number of viable rosettes at the end of reproduction (SAS Proc GLM). Traits that were included in the path model described earlier were tested. The population and water treatment terms were included in the models to control for possible differences among populations and treatments in unmeasured traits. All traits were standardized with zero means and one standard deviation for consistency with the path analysis.

Regression and path analyses were conducted separately for high- and low-elevation populations because their rosette ontogeny differed significantly (see Results). To test for differences in regression coefficients between high- and low-elevation populations, analysis of covariance was conducted, and significant interactions between morphological traits and source altitude were interpreted to indicate distinct effects of morphological traits on the expression of iteroparity between source altitudes.

In addition to path analysis and regression analysis, analysis of covariance was conducted to determine the contribution of traits to altitudinal variation in iteroparity. The same model that was used to test for altitudinal differentiation in iteroparity was used with the traits as covariates.

Postreproductive survival remained stable across water treatments, despite plasticity of the major predictor of iteroparity: the number of rosettes remaining at the end of reproduction (see Results). This result might be because traits other than the number of rosettes after reproduction independently influenced postreproductive survival. To test this hypothesis, a post hoc analysis was conducted on the residuals of postreproductive survival after we factored out the effect of the number of rosettes after reproduction. Residuals of postreproductive survival were calculated by using a logistic regression model with population, water treatment, and the number of rosettes after reproduction (SAS Proc Logistic). Multiple regression analysis was conducted on the estimated residuals by using the remaining morphological traits (SAS Proc GLM).

RESULTS

Population differentiation and plasticity of prereproductive morphological traits—Morphological traits at the prereproductive stage differed significantly between high- and low-elevation populations when plants were grown in a common environment (Table 2, Fig. 1A–C). Plants from high-elevation populations had smaller rosette diameters, but they produced more rosettes than those from low-elevation populations. Plants in wetter soil had larger rosette diameters and more rosettes, and this response was consistent for all populations. Thus, rosette diameter exhibited countergradient variation, and rosette production exhibited cogradients variation. The region effect was also significant for these traits (Table 2 and online Appendix S2). The H3 population produced fewer rosettes compared with the other high-elevation populations, and the L1 population produced more rosettes than other low-elevation populations, which is consistent with field observations (Kim and Donohue, 2011).

Population differentiation and plasticity of rosette ontogeny during the reproductive period—The pattern of rosette ontogeny varied between high- and low-elevation populations and among water treatments (Table 2). Plants from high-elevation populations decreased the number of reproductive rosettes in dry conditions, a direction consistent with cogradients variation, but those from low-elevation populations produced a relatively constant number of reproductive rosettes in all water treatments (Fig. 1D, online Appendix S2). Plants from high-elevation populations allocated a higher proportion of rosettes to reproduction in wetter conditions (Fig. 1E). In contrast, low-elevation populations allocated a smaller proportion of rosettes to reproduction under high-water conditions, whereas L1 allocated a similar proportion across water conditions.

In all populations, leaves of all reproductive rosettes degenerated during the reproductive period (data not shown). Some

nonreproductive rosettes produced at the prereproductive stage also degenerated during the reproductive period. The degree of degeneration differed between high- and low-elevation populations and among regions but not across water treatments (Table 2, Fig. 1F). Over 91% of the vegetative rosettes that existed before reproduction degenerated during the reproductive period in L2 and L3, approximately half the vegetative rosettes degenerated in L1 and H3, and fewer than 35% degenerated in H1 and H2.

Reproductive plants in all populations developed new rosettes that remained viable and vegetative throughout reproduction (Fig. 1G). Plants that experienced high-water conditions at the prereproductive stage produced more vegetative rosettes during the reproductive period (Table 2). Regional differences existed, such that L1 produced more rosettes than did other low-elevation populations (online Appendix S2).

Population differentiation and plasticity of iteroparity—Low-elevation populations produced more fruits during this single reproductive episode than did high-elevation populations (Fig. 1H, Table 2). Low-altitude populations produced more fruits under low-water conditions, whereas high-altitude populations tended to produce more fruits under high-water conditions (online Appendix S2). Consequently, low-altitude plants significantly out-performed high-altitude plants under dry conditions similar to those of their native environment.

Plants from high elevation and plants in wetter conditions had more viable rosettes after reproduction (Table 2, Fig. 1I), a pattern consistent with cogradients variation. A significant region effect and altitude \times region interaction were found, such that L1 had more rosettes at the end of reproduction compared with L2 and L3 (online Appendix S2) and thereby resembled the alpine populations. Plants from H3 had fewer rosettes compared with those from other alpine populations.

TABLE 2. Results of analysis of variance comparing morphological traits and survival between source habitats and among water treatments.

Traits	Source altitude ($F_{1, 231}$)	Water treatment ($F_{2, 231}$)	Altitude \times water ($F_{2, 231}$)	Region ($F_{2, 231}$)	Altitude \times region ($F_{2, 231}$)	Water \times region ($F_{2, 231}$)	Altitude \times water \times region ($F_{4, 231}$)
Prereproductive traits							
L	0.69	0.93	2.75	14.88***†	1.62	1.38	1.54
D	67.13***	124.85***	2.19	33.87***†	1.46	0.46	1.04
RPROD1	57.41***†	42.35***	0.74	10.86***†	9.30***†	1.21	1.45
Reproductive traits							
NREP	37.59***	25.60***	11.57***	7.41***†	1.34	2.32	0.59
RREP	0.00	0.04	15.23***	1.36	3.84*†	3.22*†	2.03
RDEG ^a	191.52***	1.22	0.12	19.01***†	6.62**	0.19	0.52
RPROD2	0.82	5.97**	0.47	5.91**†	6.51**†	0.74	1.19
Iteroparity							
FRT	36.05***†	1.14	10.00***	6.91***†	5.99**	1.24	0.29
Number of rosettes after reproduction	15.62***†	7.50***	0.25	16.50***†	10.97***	0.68	1.01
Survival ^b	23.58***	0.31	0.04	1.79	1.34	2.91	1.94

F ratios from the fixed model analysis of variance are given for morphological traits, and χ^2 values are given for survival. *Abbreviations*: L = log (leaf number per rosette); D = diameter of rosette; RPROD1 = number of rosettes produced at prereproductive stage; NREP = number of reproductive rosettes; RREP = arcsine square root (proportion of rosettes allocated to reproduction); RDEG = arcsine square root (proportion of rosettes degenerated during the reproductive period); RPROD2 = number of rosettes produced during the reproductive period; FRT = log (number of fruits).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. N = 249.

† Not significant when region is used as a random factor.

^a Ten plants that did not have any nonreproductive vegetative rosettes at the beginning of reproduction were excluded from the analysis, so the error df of the analysis was 221.

^b Mixed-model analysis of variance could not be conducted because the models did not converge.

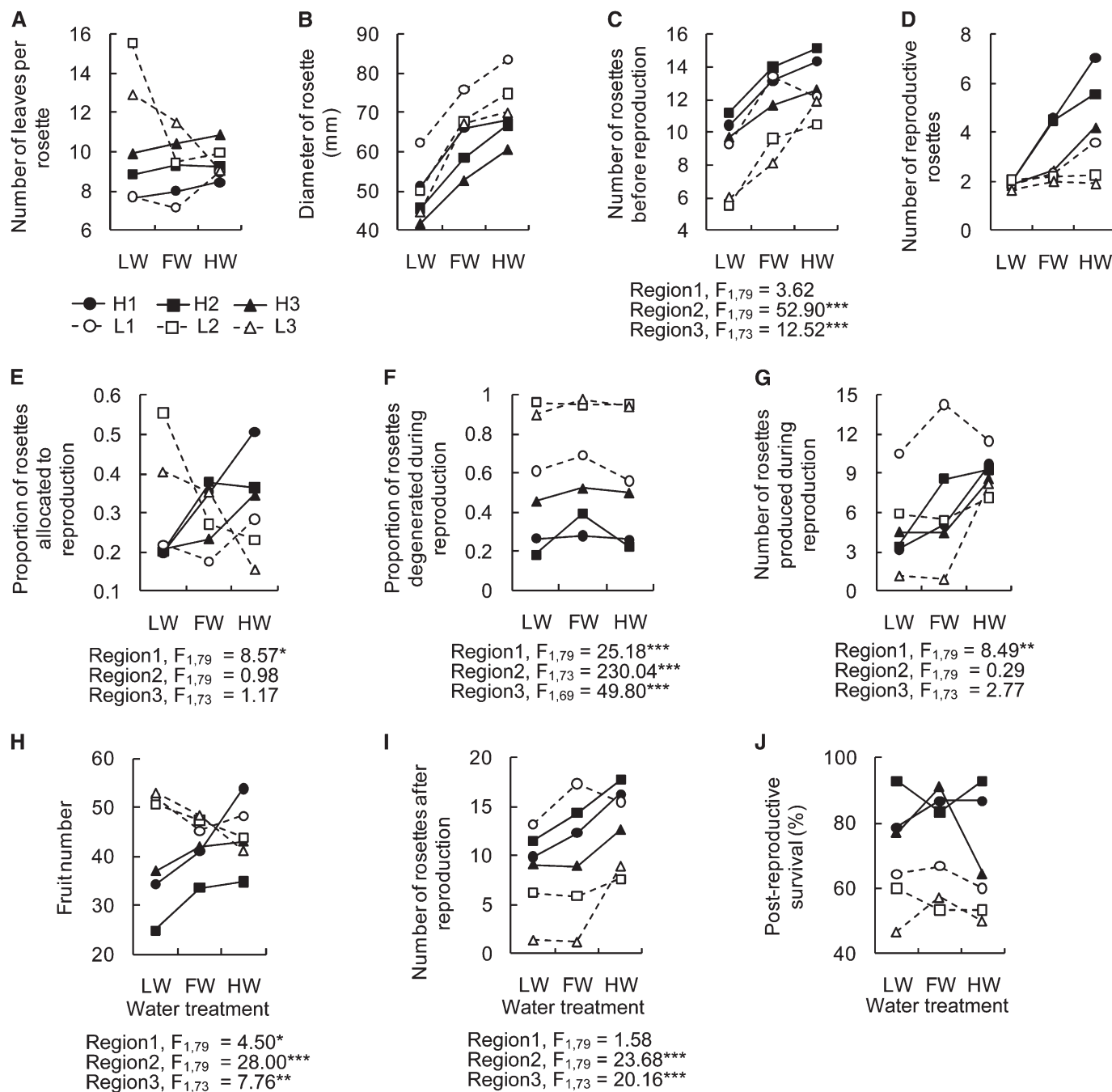


Fig. 1. Effects of source population and water availability on expression of (A) number of leaves per rosette, (B) maximum diameter of rosettes (mm), (C) number of rosettes produced at the prereproductive stage, (D) number of reproductive rosettes, (E) proportion of rosettes allocated to reproduction, (F) proportion of rosettes degenerated during the reproductive period, (G) number of rosettes produced during the reproductive period, (H) fruit number, (I) number of rosettes at the end of reproduction, and (J) postreproductive survival (%). Error bars are not presented for clarity. See Table 2 for significance tests. In each of three watersheds (regions), one population was chosen from alpine tundra sites (H1, H2, and H3), and one population was chosen from below tree line (L1, L2, and L3). F ratios (altitude) are given for each region when region \times altitude interactions were significant. Untransformed trait values are presented. FW = fluctuating water; HW = high-water; LW = low-water. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Postreproductive survival itself also differed between populations from different altitudes, consistent with field observations. Plants from high-elevation populations had significantly higher postreproductive survival than those from low-elevation populations when grown in a common greenhouse environment (Table 2, Fig. 1J). Water treatment at the prereproductive stage

did not influence postreproductive survival, as indicated by a nonsignificant water treatment effect and water \times altitude interaction.

Morphological predictors of iteroparity—Water availability influenced traits expressed at the prereproductive stage, which

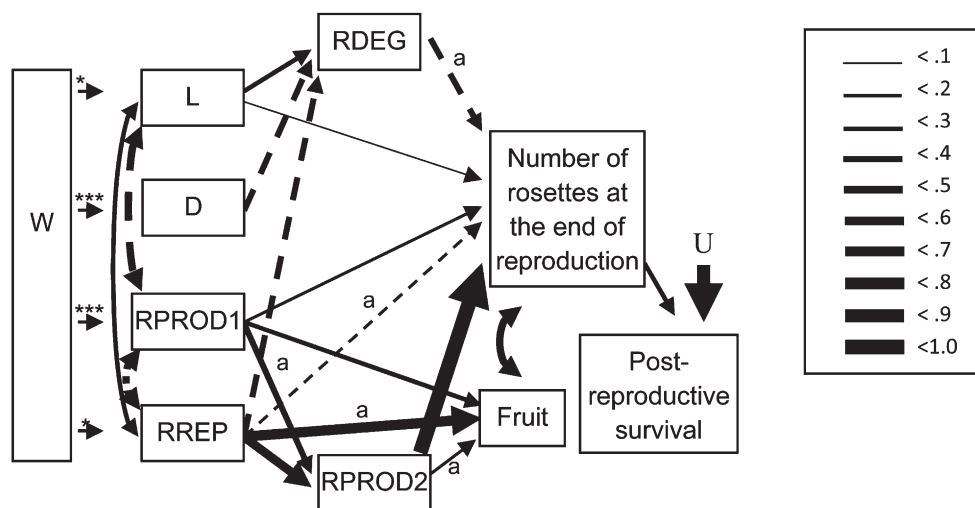
in turn influenced rosette ontogeny during the reproductive period and the number of rosettes remaining after reproduction, thereby altering postreproductive survival and the opportunity for iteroparity. However, these pathways differed between low- and high-elevation populations.

Specifically, in high-elevation populations, plants with more leaves per rosette, smaller rosette diameters, and a smaller proportion of rosettes allocated to reproduction had a higher proportion of vegetative rosettes that degenerated during the reproductive period (Fig. 2A). Plants that produced more rosettes at the prereproductive stage and allo-

cated a greater proportion of those rosettes to reproduction produced more rosettes during the reproductive period and also produced more fruits. Regarding the primary indicators of iteroparity, high-altitude plants had more rosettes at the end of reproduction if they produced more rosettes before and during reproduction and allocated a smaller proportion of rosettes to reproduction. Plants with more viable rosettes at the end of reproduction had higher postreproductive survival.

In low-elevation populations, traits expressed at the prereproductive stage did not influence the proportion of rosettes that

A High-elevation populations



B Low-elevation populations

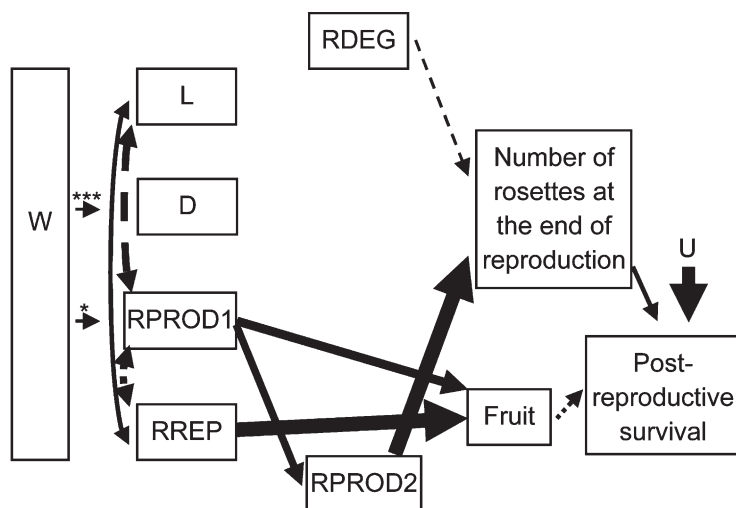


Fig. 2. Path diagram showing effects of morphological traits and fruit production on postreproductive survival. High- and low-elevation populations were analyzed separately. Only significant paths are shown. Solid lines represent positive coefficients, and dashed lines represent negative coefficients. Width of each line is proportional to the value of path coefficient (see legend) except the line between water and traits at prereproductive stage. *Figure abbreviations:* D, diameter of rosette; L, leaf number per rosette; RPROD1, number of rosettes produced at prereproductive stage; RPROD2, number of rosettes produced during the reproductive period; RDEG, proportion of rosettes degenerated during the reproductive period; RREP, proportion of rosettes allocated to reproduction; U, unknown factor. * $P < 0.05$; *** $P < 0.001$. *Significant trait by habitat interaction indicated in panel (A).

degenerated during the reproductive period (Fig. 2B). Prereproductive traits also did not contribute directly to the number of rosettes remaining at the end of reproduction, most likely because most prereproductive vegetative rosettes degenerated during the reproductive period (Fig. 1F). Plants that produced more rosettes before reproduction produced more rosettes during the reproductive period, which in turn influenced the number of rosettes remaining after reproduction, whereas total effect of prereproductive rosette production on viable rosettes remaining after reproduction was not significant (Table 3).

Fruit production was positively associated with rosette production during the reproductive period and with the number of rosettes remaining after reproduction in high-elevation populations. Those traits were not associated in low-elevation populations, indicating a lack of direct trade-offs between fruit production and vegetative growth (or maintenance). In high-elevation populations, fruit production did not affect postreproductive survival. In contrast, in low-elevation populations, fruit production had a negative effect on postreproductive survival (Fig. 2B). Because the number of rosettes before reproduction and the proportion of rosettes allocated to reproduction both had positive effects on fruit production, those prereproductive traits had an indirect negative effect on postreproductive survival in low-elevation populations.

Direct and total effects of traits on the opportunity for iteroparity sometimes differed in high-elevation plants (Table 3 vs. Fig. 2A). Although the proportion of rosettes allocated to reproduction had a direct negative effect on the number of rosettes at the end of reproduction (Fig. 2A), it also showed a negative effect on rosette degeneration during the reproductive period (which was negatively associated with rosette number after reproduction) and a positive effect on rosette production during the reproductive period (which was positively associated with rosette number after reproduction). As a consequence, plants that allocated more rosettes to reproduction had a greater number of rosettes at the end of reproduction overall.

Analysis of covariance indicated that altitudinal differences in iteroparity (i.e., postreproductive survival and the number of viable rosettes at the end of reproduction) become nonsignificant when morphological and ontogenetic traits are included in the model (Table 4). In particular, the proportion of rosettes that degenerated during the reproductive period accounted for the altitudinal variation in iteroparity, suggesting that rosette de-

generation is likely a key trait contributing to population differentiation in iteroparity in a greenhouse environment.

Post hoc residual analysis showed that the residuals of postreproductive survival did not exhibit plasticity to water (high-elevation population: $F_{2,109} = 0.50$, $P = 0.61$; low-elevation populations: $F_{2,106} = 1.49$, $P = 0.23$). However, in high-elevation populations, plants with a smaller proportion of rosettes allocated to reproduction (coefficient = -0.17 , $SE = 0.06$, $P < 0.01$) and a smaller proportion of vegetative rosette degeneration during the reproductive period (coefficient = -0.11 , $SE = 0.04$, $P < 0.01$) had higher residual survival. No trait was found to influence the residuals of postreproductive survival in low-elevation populations.

DISCUSSION

Erysimum capitatum populations exhibited variation in postreproductive survival, i.e., iteroparity, when plants were grown in a common greenhouse environment, indicating that genetic differentiation and/or maternal effects contribute to geographic variation in iteroparity. However, whereas only 2% of reproductive plants from the L2 and L3 populations survived in natural environments (Kim and Donohue, 2011), 46–60% of reproductive plants from these populations survived in the greenhouse environment, suggesting phenotypic plasticity in postreproductive mortality also contributes to in situ natural variation in life-history strategy. Prereproductive morphology and ontogeny of rosettes differed between high- and low-elevation populations, and most of them also showed phenotypic plasticity in response to water availability at the prereproductive stage, sometimes in directions consistent with cogradient variation.

Plasticity and differentiation of parity: developmental mechanisms—This experiment showed that in situ variation in life history is strongly associated with both phenotypic plasticity and population differentiation of rosette ontogeny expressed before and during the reproductive period. Although this study documented population differentiation in a common environment, it was not able to determine whether such differentiation was caused by genetic differentiation or maternal effects. Maternal effects influence trait expressions most prominently at the early life stages (Donohue, 2009), and no studies as yet have

TABLE 3. Results of simple regression analysis to determine the total contribution of morphological traits to survival and the number of vegetative rosettes after reproduction.

Trait	Survival		Number of rosettes after reproduction	
	High-elevation populations	Low-elevation populations	High-elevation populations	Low-elevation populations
L	0.12 (0.25)	−0.28 (0.20)	−0.14 (0.09)	0.00 (0.08)
D	0.59 (0.41)	0.50 (0.30)	−0.05 (0.13)	−0.22 (0.12)
RPROD1	0.09 (0.29)	0.21 (0.23)	0.25 (0.10)*	0.18 (0.10)
RREP	−0.32 (0.27)	−0.28 (0.20)	0.33 (0.09)***	0.07 (0.08)
RDEG	−0.69 (0.27)*	−0.32 (0.23)	−0.27 (0.09)***	−0.03 (0.10)
RPROD2	0.18 (0.29)	0.58 (0.25)*	0.89 (0.04)***	0.91 (0.02)***
FRT	−0.05 (0.30)	−0.54 (0.21)**	0.48 (0.09)***	0.00 (0.08)

Simple regression coefficients of standardized variables ($\pm SE$) are shown. *Abbreviations*: L = log (leaf number per rosette); D = diameter of rosette; RPROD1 = number of rosettes produced at prereproductive stage; RREP = arcsine square root (proportion of rosettes allocated to reproduction); RDEG = arcsine square root (proportion of rosettes degenerated during the reproductive period); RPROD2 = number of rosettes produced during the reproductive period; FRT = log (number of fruits). The model included population and water conditions.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

^a Significant interaction between trait and habitat.

TABLE 4. Results of analysis of covariance to test the contribution of traits to the difference in iteroparity between high- and low-elevation populations.

Trait	Postreproductive survival	Number of rosettes after reproduction
No trait	23.58***	15.62***
All traits	2.89	1.33
L	22.90***	15.29***
D	28.65***	7.31**
RPROD1	15.93***	5.90*
RREP	23.82***	16.22***
RDEG	2.58	1.77
RPROD2	25.19***	244.09***
FRT	15.03***	28.20***

The altitude effect was compared with ("All traits") and without ("No trait") traits as covariates and with each trait as a covariate separately. χ^2 values are given for postreproductive survival, and F ratios are given for the number of viable rosettes after reproduction. *Abbreviations:* L = log (leaf number per rosette); D = diameter of rosette; RPROD1 = number of rosettes produced at prereproductive stage; RREP = arcsine square root (proportion of rosettes allocated to reproduction); RDEG = arcsine square root (proportion of rosettes degenerated during the reproductive period); RPROD2 = number of rosettes produced during the reproductive period; FRT = log (number of fruits).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

demonstrated maternal effects on rosette development and degeneration, to our knowledge, suggesting that maternal effects could have limited effects on the rosette ontogeny measured in this study.

A critical difference between high- and low-elevation populations was a higher degree of degeneration of vegetative rosettes during the reproductive period in low-elevation populations. In semelparous plants, death after reproduction is hypothesized to be a highly coordinated biological process, which is often referred to as *programmed death* or *monocarpic senescence*. A key developmental mechanism for this is the degeneration of existing vegetative tissue during the reproductive period (Woolhouse, 1983; Noodén, 1988; Rose, 1991; Hensel et al., 1994; Bleecker, 1998). In *E. capitatum*, different degrees of degeneration likely have evolved in different natural populations, which resulted in differential postreproductive survival as well as number of vegetative structures at the end of reproduction.

Although postreproductive survival differed between high- and low-elevation populations, plants from semelparous populations behaved like plants from iteroparous populations in some respects. In natural environments, *E. capitatum* plants in the L2 and L3 populations do not produce vegetative rosettes during reproduction, but those in the H1, H2, H3, and L1 populations do (Kim and Donohue, 2011). In contrast, in the greenhouse, plants from the L2 and L3 populations did produce vegetative rosettes during reproduction. Given that some semelparous rosette plants exhibit iteroparity by producing viable rosettes during the reproductive period (Van Baalen and Prins, 1983; Paige and Whitham, 1987; Bender et al., 2002), the higher survival of the L2 and L3 populations in this experiment compared with those in the field is likely in part caused by the development of vegetative rosettes during the reproductive period. Although *E. capitatum* plants in the L2 and L3 populations have the developmental ability to produce vegetative rosettes during reproduction, environmental factors in their natural habitats likely inhibit the production of vegetative rosettes in situ.

Despite plasticity of morphological traits that contribute to iteroparity, postreproductive survival exhibited no plasticity to water conditions. This appears to be caused by contrasting effects of the plasticity of morphological traits on the postreproductive survival. Specifically, rosette production increased in wetter conditions in high-elevation populations, facilitating iteroparity; conversely, the proportion of rosettes allocated to reproduction was higher under wetter conditions, which had a negative effect on the residual of postreproductive survival. Thus, soil water content had both positive and negative effects on postreproductive survival through different traits, which could lead to stable postreproductive survival across variable water environments.

Effects of prereproductive traits and fruit production on life-history expression—This experiment showed that prereproductive traits significantly influenced the expression of adult life histories. Specifically, rosette production at the prereproductive stage had a positive effect on the number of rosettes remaining at the end of reproduction, directly or indirectly via rosette production during the reproductive stage. More rosettes from the prereproductive stage could directly facilitate photosynthetic capacity and the ability to produce additional rosettes during the reproductive period, but it is also possible that it is correlated with some unmeasured trait that promotes rosette production during the reproductive period.

According to life-history theory, resource-allocation trade-offs between the maintenance of vegetative tissues and fruit production, and/or between survival and fruit production, play a central role in shaping natural variation in semelparous/iteroparous life history (Gadgil and Bossert, 1970; Schaffer and Rosenzweig, 1977). In *E. capitatum*, no trade-off was found between fruit production and rosette degeneration in either high- or low-elevation populations, but higher fruit production was associated with lower postreproductive survival in low-elevation populations. In addition, fruit production and rosettes remaining at the end of reproduction explained less than 20% of variation in postreproductive survival in both high- and low-elevation populations, implying that physiological mechanisms independent of resource allocation are likely contributing to the lower survival of low-elevation populations, as in several other plant species (Noodén, 1988; Noodén et al., 1997). More study is required to test this hypothesis.

Associations between prereproductive and adult life-history traits indicate that prereproductive development and selection on prereproductive traits may influence life-history evolution in a fundamental way. In *E. capitatum* in particular, low-elevation populations produced fewer rosettes at the prereproductive stage than did high-elevation populations. Decreased leaf area has been shown to increase drought tolerance (Chaves et al., 2003; Lambers et al., 2008; McDowell et al., 2008), suggesting that dry conditions, such as those at low altitude, could select for lower leaf area in the form of reduced rosette production. A reduction in rosette production at the prereproductive stage could increase adult mortality by reducing vegetative structures at the end of reproduction because postreproductive survival in the field depends on the number and size of vegetative rosettes (Kim and Donohue, 2011). Such increased adult mortality, in turn, could promote evolution of semelparity (Charnov and Schaffer, 1973; Young, 1981; Young, 1990; Stearns, 1992). Thus, selection on rosette ontogeny, independent of life-history expression, may have consequences for the evolution of life histories.

Cogradient variation in development and life history: population consequences of plasticity to altered environments—Evidence for cogradient variation was apparent in some, but not all, traits of *E. capitatum*, such that plastic responses were in the same direction as population differentiation. For example, plants in drier conditions produced fewer rosettes at the prereproductive stage, and low-elevation populations, which inhabit drier sites, produced fewer rosettes than high-elevation populations. However, other traits, such as prereproductive rosette diameter, exhibited counter-gradient variation. Such trait-specific co- and counter-gradient variation is also reported in other plant species (Eckhart et al., 2004; Conover et al., 2009; Gonzalo-Turpin and Hazard, 2009). Because both cogradient and counter-gradient traits would contribute to absolute fitness, it is necessary to test the adaptive significance of those traits simultaneously to predict plant performance under contrasting environments.

The observed plasticity in prereproductive rosette production is predicted to influence life-history expression in response to altered soil water conditions. Indeed, like prereproductive rosette production, the trait most closely associated with iteroparity—the number of rosettes remaining after reproduction—also showed cogradient variation in response to soil water content experienced at the prereproductive stage. If conditions become drier in alpine habitats as predicted (Taylor and Seastedt, 1994; Harte et al., 1995; Calanca, 2007; Lambrecht et al., 2007), *E. capitatum* is expected to produce fewer vegetative rosettes at the prereproductive stage, which would result in fewer viable rosettes at the end of reproduction. Because postreproductive survival in the field depends on the number and size of vegetative rosettes (Kim and Donohue, 2011), such plastic responses of high-elevation plants could result in higher adult mortality rates and a more semelparous life history, even without acute drought stress. Changes in life-history strategy are expected to influence population demography, such that seedling recruitment and a rapid transition to reproduction will contribute to population growth rate more than they would currently (Silvertown et al., 1993).

Although high-elevation plants exhibited phenotypes similar to those of low-elevation semelparous plants in dry conditions, plasticity to dry conditions alone does not produce a semelparous plant such as those found at low elevation. In particular, nonreproductive rosette degeneration during the reproductive period was pronounced in low-elevation populations. This result suggests that degeneration, rather than being a component of (potentially adaptive) plasticity in response to water availability, may have evolved separately under conditions in which vegetative rosettes seldom contributed to postreproductive survival.

Summary and conclusion—In *E. capitatum*, traits associated with iteroparity exhibited evidence of population differentiation as well as phenotypic plasticity in response to water availability. Changing patterns of soil moisture in alpine environments are therefore expected to change life-history expression, which would, in turn, influence population demography. In addition, the contribution of prereproductive traits to iteroparity suggests that natural selection on juvenile traits could contribute to geographic variation in life history in this system as much as would selection on adult reproductive strategy per se. Although high-elevation populations are expected to exhibit a more semelparous life history in dry conditions, it is unclear whether that would be adaptive. Explicit tests of the adaptive value of semelparity would require examining natural or manipulated life-history variation under different conditions and monitoring fitness over the whole lifespan of these perennials.

LITERATURE CITED

- BENDER, M. H., J. M. BASKIN, AND C. C. BASKIN. 2002. Phenology and common garden and reciprocal transplant studies of *Polymnia canadensis* (Asteraceae), a monocarpic species of the North American deciduous forest. *Plant Ecology* 161: 15–39.
- BLEECKER, A. B. 1998. The evolutionary basis of leaf senescence: Method to the madness? *Current Opinion in Plant Biology* 1: 73–78.
- BRIDLE, J. R., AND T. H. VINES. 2007. Limits to evolution at range margins: When and why does adaptation fail? *Trends in Ecology & Evolution* 22: 140–147.
- BYARS, S. G., W. PAPST, AND A. A. HOFFMANN. 2007. Local adaptation and cogradient selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution; International Journal of Organic Evolution* 61: 2925–2941.
- CALANCA, P. 2007. Climate change and drought occurrence in the Alpine region: How severe are becoming the extremes? *Global and Planetary Change* 57: 151–160.
- CAMPBELL SCIENTIFIC INC. 2001. Hydrosense instruction manual. Campbell Scientific, Logan, Utah, USA.
- CHARMANTIER, A., R. H. MCCLEERY, L. R. COLE, C. PERRINS, L. E. B. KRUIK, AND B. C. SHELDON. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320: 800–803.
- CHARNOV, E. L., AND W. M. SCHAFFER. 1973. Life-history consequences of natural selection: Cole's result revisited. *American Naturalist* 107: 791–793.
- CHAVES, M. M., J. P. MAROCO, AND J. S. PEREIRA. 2003. Understanding plant responses to drought—From genes to the whole plant. *Functional Plant Biology* 30: 239–264.
- CLAUSSEN, J. D., D. KECK, AND W. M. HIESEY. 1940. Experimental studies on the nature of species. I. The effect of varied environment on western North American plants. Carnegie Institute of Washington, Washington, D.C., USA.
- CONOVER, D., AND E. T. SCHULTZ. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology & Evolution* 10: 248–252.
- CONOVER, D. O., T. A. DUFFY, AND L. A. HICE. 2009. The covariance between genetic and environmental influences across ecological gradients. *Annals of the New York Academy of Sciences* 1168: 100–129.
- DIAZ, H. F., AND J. K. EISCHEID. 2007. Disappearing “alpine tundra” Köppen climatic type in the western United States. *Geophysical Research Letters* 34: L18707–L18711.
- DONOHUE, K. 2009. Completing the cycle: Maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 364: 1059–1074.
- ECKHART, V. M., M. A. GEBER, AND C. M. MCGUIRE. 2004. Experimental studies of adaptation in *Clarkia xantiana*. I. Sources of trait variation across a subspecies border. *Evolution; International Journal of Organic Evolution* 58: 59–70.
- ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton University Press, Princeton, New Jersey, USA.
- FRANCO, M., AND J. SILVERTOWN. 1996. Life history variation in plants: An exploration of the fast–slow continuum hypothesis. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 351: 1341–1348.
- GADGIL, M., AND W. H. BOSSERT. 1970. Life historical consequences of natural selection. *American Naturalist* 104: 1–24.
- GEBER, M. A., AND L. R. GRIFFEN. 2003. Inheritance and natural selection on functional traits. *International Journal of Plant Sciences* 164 (Supplement 3): S21–S42.
- GONZALO-TURPIN, H., AND L. HAZARD. 2009. Local adaptation occurs along altitudinal gradient despite the existence of gene flow in the alpine plant species *Festuca eskia*. *Journal of Ecology* 97: 742–751.
- HARTE, J., M. S. TORN, F.-R. CHANG, B. FEIFAREK, A. P. KINZIG, R. SHAW, AND K. SHEN. 1995. Global warming and soil microclimate: Results from a meadow-warming experiment. *Ecological Applications* 5: 132–150.

- HENSEL, L. L., M. A. NELSON, T. A. RICHMOND, AND A. B. BLEEKER. 1994. The fate of inflorescence meristems is controlled by developing fruits in *Arabidopsis*. *Plant Physiology* 106: 863–876.
- HOLT, R. D. 1990. The microevolutionary consequences of climate change. *Trends in Ecology & Evolution* 5: 311–315.
- JUMP, A. S., AND J. PEÑUELAS. 2005. Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letters* 8: 1010–1020.
- KIM, E., AND K. DONOHUE. 2011. Demographic, developmental and life-history variation across altitude in *Erysimum capitatum*. *Journal of Ecology* 99: 1237–1249.
- KIRKPATRICK, M., AND N. H. BARTON. 1997. Evolution of a species' range. *American Naturalist* 150: 1–23.
- KÖRNER, C. 2003. Alpine plant life: Functional plant ecology of high mountain ecosystems. Springer-Verlag, Berlin, Germany.
- LAMBERS, H., T. L. PONS, AND F. S. CHAPIN III. 2008. Plant physiological ecology. Springer Verlag, New York, New York, USA.
- LAMBRECHT, S. C., M. E. LOIK, D. W. INOUE, AND J. HARTE. 2007. Reproductive and physiological responses to simulated climate warming for four subalpine species. *New Phytologist* 173: 121–134.
- LEVINS, R. 1968. Evolution in changing environments: Some theoretical explorations. Princeton University Press, Princeton, New Jersey, USA.
- LINHART, Y. B., AND M. C. GRANT. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27: 237–277.
- MCDOWELL, N., W. T. POCKMAN, C. D. ALLEN, D. D. BRESHEARS, N. COBB, T. KOLB, J. PLAUT, ET AL. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.
- MCINTYRE, G. I. 1977. The role of nutrition in apical dominance. In D. H. Jennings [ed.], Integration of activity in the higher plant, 251–273. Cambridge University Press, Cambridge, UK.
- MINER, B. G., S. E. SULTAN, S. G. MORGAN, D. K. PADILLA, AND R. A. RELYEA. 2005. Ecological consequences of phenotypic plasticity. *Trends in Ecology & Evolution* 20: 685–692.
- MITCHELL, R. J. 2001. Path analysis. In S. M. Scheiner and J. Gurevitch [eds.], Design and analysis of ecological experiments. Oxford University Press, Oxford, UK.
- NOODÉN, L. D. 1988. Whole plant senescence. In L. D. Noodén and A. C. Leopold [eds.], Senescence and aging in plants. Academic Press, London, UK.
- NOODÉN, L. D., J. J. GUIAMET, AND I. JOHN. 1997. Senescence mechanisms. *Physiologia Plantarum* 101: 746–753.
- PAIGE, K. N., AND T. G. WHITHAM. 1987. Flexible life history traits: Shifts by scarlet gilia in response to pollinator abundance. *Ecology* 68: 1691–1695.
- PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37: 637–669.
- PARRY, M. L., O. F. CANZIANI, J. P. PALUTIKOF, P. J. VAN DER LINDEN, AND C. E. HANSON. 2007. Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change, 2007. Cambridge University Press, New York, New York, USA.
- PRICE, R. A. 1987. Systematics of the *Erysimum capitatum* alliance (Brassicaceae) in North America. Ph.D. dissertation, University of California, Berkeley, Berkeley, California, USA.
- ROCHOW, T. F. 1970. Ecological investigations of *Thlaspi alpestre* L. along an elevational gradient in the central Rocky Mountains. *Ecology* 51: 649–656.
- ROLLINS, R. C. 1993. The Cruciferae of continental North America: Systematics of the mustard family from the Arctic to Panama. Stanford University Press, Stanford, California, USA.
- ROSE, M. R. 1991. Evolutionary biology of aging. Oxford University Press, Oxford, UK.
- SAKAI, A. K., F. W. ALLENDORF, J. S. HOLT, D. M. LODGE, J. MOLOFSKY, K. A. WITH, S. BAUGHMAN, ET AL. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–332.
- SCHAFER, W. M., AND M. L. ROSENZWEIG. 1977. Selection for optimal life histories II: Multiple equilibria and the evolution of alternative reproductive strategies. *Ecology* 58: 60–72.
- SILVERTOWN, J. W., M. FRANCO, I. PISANTY, AND A. MENDOZA. 1993. Comparative plant demography—Relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81: 465–476.
- STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.
- SULTAN, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology* 21: 127–178.
- TAYLOR, R. V., AND T. R. SEASTEDT. 1994. Short- and long-term patterns of soil moisture in alpine tundra. *Arctic and Alpine Research* 26: 14–20.
- THEURILLAT, J.-P., AND A. GUISAN. 2001. Potential impact of climate change on vegetation in the European Alps: A review. *Climatic Change* 50: 77–109.
- VAN BAALEN, J., AND E. G. M. PRINS. 1983. Growth and reproduction of *Digitalis purpurea* in different stages of succession. *Oecologia* 58: 84–91.
- VERKAAR, H. J., AND A. J. SCHENKEVELD. 1984. On the ecology of short-lived forbs in chalk grasslands: Semelparity and seed output of some species in relation to various levels of nutrient supply. *New Phytologist* 98: 673–682.
- WALTHER, G.-R. 2003. Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 169–185.
- WOOLHOUSE, H. W. 1983. Hormonal control of senescence allied to reproduction in plants. In W. J. Meudt [ed.], Beltsville symposia in agricultural research: Strategies of plant reproduction. Allanheld, Osmun & Co. Publishers, Montclair, New Jersey, USA.
- YOUNG, T. P. 1981. A general model of comparative fecundity for semelparous and iteroparous life histories. *American Naturalist* 118: 27–36.
- YOUNG, T. P. 1990. Evolution of semelparity in Mount Kenya lobelias. *Evolutionary Ecology* 4: 157–171.
- YOUNG, T. P., AND C. K. AUGSPURGER. 1991. Ecology and evolution of long-lived semelparous plants. *Trends in Ecology & Evolution* 6: 285–289.