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The Effects of Genetic and Environmental Variation on Growth and Flowering

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Abstract

The ability to respond to seasonal cues, including changes in daylength and temperature, can be vital for sessile organisms. One of the mechanisms plants use to deal with seasonal variation is adjusting their allocation to vegetative growth and reproduction, and the timing of the transition to flowering. To respond to selection and adapt to changing environments, populations must harbor genetic variation for these traits. This research addresses the following questions: (1) How much quantitative genetic variation for flowering time exists within a population? (2) Does photoperiod affect the timing of and allocation to growth and flowering? (3) Is their genetic variation and genetic correlations among and within photoperiod treatments for growth and flowering? To address these questions, we used a single population of the North American wildflower, *Mimulus guttatus.* We grew open-pollinated, field collected seed in a greenhouse to assess the standing genetic variation for growth and flowering traits. We then created full-sib families through assortative mating by flowering time. We grew seed in growth chambers in three photoperiod treatments (13, 14, and 15 hour days, corresponding to early spring through summer). We found substantial variation in flowering time across environments and maternal families. Additionally, we found that plants allocated their resources towards flowering and clonal growth differently according to daylength. Together, these results suggest that a single population can harbor substantial genetic variation, and that this variation may be the target of selection as climates shift and the onset of spring advances.

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Introduction

One of the most fundamental questions faced by all organisms is: when is the best time to reproduce to maximize survival and success of their offspring. As sessile organisms, it is important for plants to be able to respond to seasonal cues and variable environments, so that they may correctly time their transition to reproductive growth (Cohen 1976). Population flowering phenologies need to be synchronized so that potential mates are flowering; and flowering plants that rely on pollinators must display flowers when the appropriate pollinators are active (Grant 1971; Waser and Real 1979; Rathcke and Lacey 1985). In addition, life history theory predicts that selection on flowering time includes the trade-off between allocation to vegetative growth versus allocation to flowering and maturing seed (Cohen 1976; Kozlowski 1992), and that different environments might favor alternate strategies of the timing of growth versus reproduction (Johnasson *et al*. 2013). For all of these reasons, adaptation of plant species to new biotic and abiotic environments often involves evolution of flowering time (Elzinga *et al.* 2007; Sandring *et al.* 2007).

The evolution of flowering time can occur very rapidly (e.g. Primack *et al*. 2004; Franks *et al.* 2007) due to phenotypic plasticity and/or genetic evolution. Various environmental factors can influence flowering time through a plastic response (e.g. Vermeulen 2015), through direct selection on flowering time itself (e.g. Franks *et al*. 2007), or through indirect selection caused by genetic correlations with other traits (e.g. Agrawal *et al*. 1999). The ability of plant species to react quickly to selection on flowering time suggests that populations harbor substantial quantitative genetic variation for flowering responses. Various forms of heterogeneous natural selection, as well as the genetic architecture of traits can affect the quantitative genetic variation within a population. Spatial or temporal variation in selection within a population can maintain

genetic variation (Levene 1953; Delph and Kelly 2014), and there is abundant evidence that selection varies among microsites within contiguous plant populations (e.g. Stewart and Schoen 1987; Mojica *et al.* 2012). Alternatively, selection may favor different genotypes in different environments, particularly if there are gene x environment interactions so that genotypes respond differently to environmental variation (Via and Lande 1985; Gillespie and Turelli 1989). In addition, epistatic interactions among loci can maintain variation when the fitness effects of an allele change depending on an allele at another locus (Weinig *et al.* 2003). Finally, if the genetic covariances amongst traits under selection are such that alleles affect some traits positively and others negatively, then these alleles will tend to remain at intermediate frequencies longer (Houle 1991).

Negative genetic covariances amongst traits, or trade-offs, are a fundamental feature of life history theory (Stearns 1977; Ågren *et al.* 2013). Trade-offs may arise when two or more traits are both under selection to increase, but share a limiting resource; common examples include flower size and number (Worley and Barrett 2000), or increased egg size and number (Fox *et al*. 1997). In plants, a trade-off may also exist between vegetative growth and flowering if an individual cannot simultaneously allocate resources to both growth and reproduction (Reekie and Bazzaz 1987; Kozlowski 1992; Obeso 2002). Trade-offs may also arise directly through meristem usage, whereby a meristem can either take on vegetative fate or reproductive fate, but not both (Geber 1990). Friedman *et al.* (2015) have shown that populations that invest heavily in vegetative growth, specifically clonal growth, take longer to flower. Additionally, Van Drunen and Dorken (2012) found that investing in reproductive growth limits investment in clonal growth. For clonal plants, this trade-off between sexual and asexual growth represent

alternate routes to fitness, that may have different consequences depending on the environment (Reekie and Bazzaz 2005; Van Drunen *et al.* 2015).

Classical life-history models predict that vegetative growth precedes reproduction during the course of a season, because the longer a plant delays flowering, the longer and larger it can grow and secure resources for reproduction (Iwasa and Cohen 1989; Ejsmond *et al.* 2010; Weis *et al*. 2014). However, too long a delay can impede the plant from setting any viable seed, if the season turns unfavorable. How plants partition resources between vegetative growth and reproduction should thus depend on both the ontogeny of the plant and the environment or the season it experiences. As sessile organisms, it is crucial that plants be able to respond to their environment, and indeed many traits show phenotypic plasticity as a response to variable environments (Bradshaw 1965; Schlichting 1986; Via *et al.* 1995). Phenotypic plasticity is considered adaptive if plastic genotypes have the greatest global fitness across environments (Via and Lande 1985; Via *et al.* 1995). For selection to act on phenotypic plasticity, there needs to be significant genetic variation in plasticity, often measured as genotype x environment interactions. Plants are faced with both intra- and inter-annual variability in their environments, and many phenological traits show plasticity in their response to this seasonal variability (van Kleunen and Fischer 2001).

Optimal flowering phenology depends strongly on local climatic and ecological conditions. As such, many temperate plants rely on a combination of seasonal cues to transition from vegetative to reproductive growth. Seasonal cues that drive this transition include temperature, winter exposure (vernalization), and daylength (photoperiod) (Rathcke and Lacey 1985; Lempe *et al.* 2005; Romera-Branchat *et al.* 2014). Photoperiod is the one seasonal cue that does not show inter-annual variation, regardless of other climatic factors; therefore, it is a

reliable cue that many temperate plants use to determine the time to transition to their reproductive phase (Lacey 1988; Koornneef *et al.*1991). However, as climates change, and springs advances earlier, plants are confronted with warmer temperatures at shorter daylengths (Amano *et al.* 2010; Wilczek *et al.* 2010). How this de-coupling between photoperiod and temperature affects flowering phenology, and early season trade-offs between vegetative growth and reproduction, remains an open question.

In this study, we use the wildflower *Mimulus guttatus* (Phrymaceae) to study variation in flowering time and vegetative growth. *Mimulus guttatus* makes a good study system for such questions because the species is known to exhibit substantial variation in flowering time and vegetative growth among different populations (Vickery 1978; Hall and Willis 2006). This variation has largely been driven by local adaptation to seasonally dry environments (Lowry *et al.* 2008; Ivey and Carr 2012; Kooyers *et al.* 2014). Such ecological differences have imposed strong selection for changes in flowering time and allocation to vegetative growth, resulting in the advent of annual and perennial ecotypes (Vickery 1978; Hall and Willis 2006; Lowry *et al.* 2008). This study investigates the standing quantitative genetic variation within a single perennial population of *M. guttatus* and the effects of changing or seasonal environments on growth and flowering.

Here, we investigate whether there is genetic variation and phenotypic plasticity for the response to daylength in the timing of growth and flowering in a single population of *M. guttatus*. Our first goal was to measure the quantitative genetic variation for flowering time within the population in a common greenhouse environment. Next, we grew full-sib maternal families in three photoperiod treatments to assess how photoperiod affects the timing of and allocation to growth and flowering. The study addresses the following questions: (1) How much

quantitative genetic variation for flowering time exists within a population? (2) Does photoperiod affect the timing of and allocation to growth and flowering? (3) Is there genetic variation and genetic correlations among and within photoperiod treatments for growth and flowering? Understanding how plants may respond to environmental cues is important in understanding how they may adapt to changing environments. It is particularly relevant that we study the standing quantitative genetic variation for these responses, as this is the material upon which immediate selection can act.

Methods

Study species. The North American wildflower *Mimulus guttatus* (Phrymaceae), the common monkey flower, is a hermaphroditic herbaceous plant widely distributed in moist sites across western North America. The species shows extensive morphological variation, with populations classified as having either annual or perennial strategies (Vickery 1978). Although there is some disagreement about their taxonomic status (Nesom 2012), the two types are fully interfertile. For this study, we used a perennial population located in northern California, near Mt. Shasta at N122.176, W41.1105. In August 2013, we collected open pollinated seed from 30 plants, to be used in subsequent experiments. Plants were selected randomly, making sure that they were at least 100cm apart to limit the likelihood of sampling clones.

Greenhouse experiment. To classify the genetic variation in flowering time in the population of interest, we grew seed from maternal families in a controlled greenhouse environment. In January 2015, we planted ten seed from 27 open-pollinated field-collected families (N=270) in 5

cm pots filled with moist Fafard 4P growing mix. We randomized the position of pots within 13 flats. The seeds were stratified in the dark at 4°C for 5 days. We then moved the pots into the rooftop greenhouse at Syracuse University. The greenhouse was held at 21°C during the day and 18°C during the night, with a 16-hour photoperiod. Flats were misted twice daily until germination and bottom watered every day for 1 hour. Plants were monitored for germination and date of first flower.

We created outcrossed seed families for subsequent experiments by crossing 64 unrelated individuals (i.e. we avoided crossing half siblings). Because variation within a population in flowering time can cause assortative mating (Devaux and Lande 2008; Weis 2005), we created three sets of crosses, with individuals within each set chosen randomly. We crossed individuals that flowered early with other early flowering individuals; late flowering individuals with other late flowering individuals; and early flowering individuals with late flowering individuals (we randomly assigned whether the early or late parent was the mother to avoid maternal effects). We allowed seed to ripen on the mother plant, and then collected it and stored it at room temperature until use in the next experiment.

Growth chamber experiment. To investigate how variation in vegetative growth and flowering time are influenced by quantitative genetic variation and seasonal environmental variation, we grew outcrossed full-sib plants that originated from a single population in three replicate growth chambers that varied in their photoperiod. Because the seed originated from maternal plants that experienced similar greenhouse conditions and after-ripening environments (see above), we assume there were minimal maternal effects.

To investigate one aspect of seasonal variation, we used three growth chambers (Conviron E15) that varied in their photoperiod with day lengths of 13 hours 5 minutes, 14 hours 5 minutes, and 15 hours 5 minutes. We chose these day lengths to simulate the day lengths of early spring (April 8th), late spring (May 3rd), and the longest day of the year (June 21st) in the natural location of this population. The temperature in all treatments was constant at 21°C days, 18°C nights. We used 30 seed from 6 early x early crosses, 7 early x late crosses, and 6 late x late crosses (N=570). We randomly assigned the 570 seed to the three treatments, while explicitly keeping the number of seed per family equal in each treatment. In July 2015, we planted seed in 5cm pots filled with moist Fafard 4P growing mix. We stratified seed in the dark at 4°C for 7 days, and then moved the flats into their assigned growth chamber treatment. We misted pots twice daily until germination and bottom watered every day for 1 hour. Although the growth chambers were identical models there may have been unwanted variation between them. To minimize this, we rotated the plants among the different chambers (maintaining their assigned treatment settings), and shuffled the position of every flat within a treatment every three days. There were 6 flats per treatment and 32 pots per flat, however one flat per treatment only contained 31 pots (n=191 per treatment). Each flat was considered a block in later statistical analyses.

We monitored plants daily for germination and date of first flower. Additionally, we measured the following morphological traits every 2 weeks: leaf length, stolon number, stolon length, and leaf number. On the day of first flowering, we recorded node of first flower, length of the first three internodes, third leaf length, stolon number, and stolon length. At 2 weeks after first flowering, we measured branch number, stolon number, height, and flower number. We harvested flowering plants at 4 weeks after they first flowered, and recorded the number of

flowers and whether they were located on the primary axis, primary branches or stolons. We collected all of the nonflowering plants at 14 weeks (which coincided with the last harvest point of flowering plants) and recorded them as such. For all plants, we harvested the above ground biomass, separated it by branch type (primary axis, primary branch, or stolon), dried it, and weighed it.

Statistical analysis. To estimate genetic variation (V_G) and broad-sense heritability (H^2), in flowering time for greenhouse-grown plants, we used a general linear mixed model (SAS PROC MIXED; 9.4; SAS Inst. 2014), with family as a random effect. We estimated genetic variance as four times the family variance component (for a half-sib design), and calculated the broad-sense heritability as the estimated genetic variance divided by the total phenotypic variance (Lynch and Walsh 1998).

For all growth chamber plants, we investigated the relationship between vegetative traits and flowering traits by calculating phenotypic correlations among the traits for plants in each daylength treatment (SAS PROC CORR).

We examined the effect of photoperiod treatment on each measure of flowering and growth traits separately using a general linear mixed model (SAS PROC MIXED). For this model, treatment was a fixed effect, while family, treatment by family interaction, and block nested within treatment were random effects. We used restricted maximum likelihood (REML) to estimate the variance components of the random effects, and their significance was determined using the likelihood-based *Wald Z*-scores, which are computed as the parameter estimate divided by its asymptotic standard error (Littell *et al.* 1996). Although we are not specifically interested

in the effect of cross, we ran a model that included cross type as a fixed effect and excluded family.

To estimate genetic variation (V_G) and broad-sense heritability (H^2), we used a general linear mixed model (SAS PROC MIXED) for each trait and each treatment separately, with family and block as random effects. We estimated genetic variance as two times the family variance component (for a full-sib design), and calculated the broad-sense heritability as the estimated genetic variance divided by the total phenotypic variance. We calculated family means using Best Linear Unbiased Predictors (BLUPs).

To estimate pairwise genetic correlations for sets of traits, we first standardized data to z-scores (mean=0, standard deviation=1) and performed restricted maximum likelihood general linear mixed models (SAS PROC MIXED) for each pair of traits within each treatment. The model included the effects of family and block as random effects. We specified the covariance matrix to be "unstructured", allowing both among- and within-family variances and covariances to differ between traits. Then the genetic correlation between traits (r_G)—defined as $COV_G/(V_{G1}V_{G2})^{1/2}$, can be calculated directly from the observational variances and covariance between traits. We present both raw *P*-values, and adjusted values for multiple testing using the Bonferonni correction.

To investigate the differences between treatments in growth over time, we used a random regression mixed model in SAS PROC MIXED using standardized values for leaf length, leaf number, and stolon number. We fit individual intercepts and slopes for each family and used a repeated measures design. Because the data did not show a linear increase over time, we included both the linear and quadratic effects of time. Thus, the model included fixed effects of time, time x time, treatment, and their interactions. We included block nested within treatment as

a random effect. We included family as a random effect, and allowed among-family and within-family variances to differ between treatments. For each trait and treatment, we obtained a line of best fit based on family BLUPs.

Results

Intrapopulation variation in a common environment. Plants grown from field-collected open-pollinated seed in the greenhouse showed a broad distribution of flowering phenology (mean=40.71 days, SD=5.67 days, range=31-66 days, n=260). In addition, 16 plants, from 7 different maternal families, failed to flower at all over the 14 weeks that the plants were maintained. There was a significant effect of family for flowering time (V_G=29.99 days), with a broad-sense heritability (H^2) estimate of 0.54.

Correlations between flowering time and vegetative growth in growth chamber treatments. Plants grown in growth chambers that differed in daylength, showed similar phenotypic correlations among flowering time traits, vegetative growth traits, and biomass allocation (Table 1), with most traits showing significant correlations. Flowering time is negatively correlated with total flower number (at 4 weeks post-flowering), indicating that early flowering plants are making more flowers overall. Flowering time is also negatively correlated with early growth leaf size (at 2 weeks post-germination), showing that plants that flower early also grow more rapidly at early stages. In all three treatments, the correlations between flowering time and stolon traits were positive (early flowering plants produce few stolons).

The effect of daylength on flowering and vegetative growth. Overall, the highest proportion of plants flowered in the 15-hour treatment (83%), an intermediate proportion in the 14-hour treatment (56%), and the lowest in the 13-hour treatment (20%). We found a significant effect of treatment for all traits included in the model (Table 2), indicating that all traits showed significant phenotypic plasticity (Figure 1). In the model that included cross, we found a significant effect of cross for flowering time (F stat=$13.16_{2,546}$, P<.0001), but no significant cross x treatment interaction. In addition, the effect of family was significant for all traits. The three biomass traits—stolon mass, branch mass, and primary axis mass, showed significant genotype by environment interactions (family x treatment effect, Table 2C), indicating that different families showed different degrees of plasticity.

Genetic correlations and heritability. Genetic correlations were of the same sign and similar magnitude across all three treatments. Strong genetic correlations were found between leaf length at week 2 and flowering time, total flower number and flowering time, and flower number and stolon number (Table 3), the latter two remaining highly significant even after adjusting for multiple testing. The correlation between flower number and flowering time was especially high (13 hrs.=-0.81, 14 hrs.=-0.95, 15 hrs.=-0.94), as was flower number and stolon number (13 hrs.=-0.97, 14 hrs.=-0.77, 15 hrs.=-0.77; Table 3). Stolon mass and primary rosette mass were not significantly correlated in any of the three treatments. All traits showed strong effects of family (Table 2) and significant genetic variation. Broad-sense estimates of heritability were high for all traits across all treatments, however estimates were lower for stolon number in the 13 hour treatment (H^2=0.19; Table 4).

The effect of daylength on growth rate. The growth of plants over time differed significantly between the treatments (Table 5). For leaf size, treatment explained a small, but statistically significant proportion of the variation (Table 5; Figure 2A). Leaf number and stolon number were more strongly influenced by treatment (Table 5; Figure 2). Plants in the 13- and 14-hour treatments had a greater number of leaves than the 15-hour treatment in the early life stages; however this pattern reversed in later life stages (Figure 2B). We found the opposite to be true for stolon number. Plants in the 13 hour treatment had fewer stolons than the 14 and 15 hour treatment in the early life stages; however plants in the 13 hour treatment had the greatest number of stolons in later life stages (Figure 2C).

Discussion

The main findings of our study demonstrate that there is both genetic variation and phenotypic plasticity for flowering time, and vegetative and flowering responses to daylength, within a single population of *M. guttatus.* This population harbors significant variation in growth and reproduction. We found a significant treatment x family interaction for biomass traits, indicating a genotype x environment interaction (Table 2; Figure 2E-F). As predicted by life history theory, we found a trade-off between vegetative and reproductive growth as indicated by negative genetic correlations between components of these traits (Table 3). Finally, daylength also significantly affected growth rate, such that plants grown in the shorter daylengths grew slower early in life but allocated more towards clonal growth later in life, while plants grown in the longer daylength grew rapidly early in life and allocated preferentially towards their main rosette (Figure 2). Below we discuss the implications of these findings for our understanding of

trade-offs between vegetative growth and reproduction, and responses to selection in changing environments.

Environment-dependent allocation to growth and flowering. Photoperiod and temperature are two of the main abiotic cues that plants use to transition from vegetative to reproductive growth. A recent study by Li *et al.* (2014) investigated the underlying genetic variation in *Arabidopsis thaliana* for response to temperature. They found that a 1-3 degree increase in seasonal temperature decreased flowering. This study is of particular importance, as it predicts flowering phenologies in response to one of the important environmental cues that plants respond to. Our study, addresses the other important cue, daylength. It is well known that daylength plays a critical role in growth and flowering (Romera-Branchat *et al.* 2014). Fitting with these expectations, daylength significantly affected growth and reproduction in our study. Plants invested heavily in vegetative growth in short daylengths and allocated preferentially towards reproductive growth in the longer photoperiod (Table 1). In the natural population, plants are receiving the cue to grow vegetatively early in spring, when daylength is short. As the days get longer, they receive the appropriate environmental cues to begin their transition from vegetative to reproductive growth. A recent study by Friedman and Willis (2013) shows that the critical photoperiod required for flowering is highly variable across different populations of *M. guttatus*. Here we show that within a single population, maternal families also respond differently to daylength (Table 2; Figure 1). These differential responses indicate that there is genetic variation within this population that selection may act on, which may explain the differences in the proportion of flowering individuals across photoperiods.

Being able to respond to their environment is particularly important for sessile organisms, like plants. By maintaining this ability to respond, plants can respond to differences in the

environment over the course of a growing season. A study by Debieu *et al.* (2013) investigated the genetic variation in seed dormancy, vegetative growth rate, and flowering time in *Arabidopsis thaliana* across a latitudinal gradient. They found that the co-variation between these three traits follows a latitudinal cline, such that at high latitudes growth rate is positively correlated with seed dormancy and negatively correlated with flowering time. In our study, we found that daylength had a significant effect on the rate of growth, such that plants grown under the 13-hour daylength initially grew leaves more rapidly than those in the 15-hour daylength; however, this shifted in later life stages when the plants in the 13-hour photoperiod invested more in clonal growth than leaf growth (Table 5; Figure 2). In the peak of the growing season plants are allocating resources towards their main rosette which ultimately indicates an investment in reproductive growth and flowering. Early in the growing season, plants are allocating preferentially towards vegetative and clonal growth.

Our growth rate results suggest that there may be heterogeneous selection over time; which may be one mechanism by which genetic variation is maintained. Selection pressures may vary throughout the growing season; and families may respond differently to the changes in daylength throughout the growing season. For later flowering families, early vegetative and clonal growth may increase viability and fitness later in the growing season. For early flowering families, rapid flowering early in the growing season results in a greater number of flowers overall and thus higher fitness through sexual reproduction. Selection may also vary spatially throughout the population, such that microsites within the population experience different selection, resulting in maternal families that respond differently to daylength. While seed dispersal is extensive in this species, clonal growth remains within the immediate proximity of the mother plant. This may result in families that inhabit the same microsite as their ramets. This

variation in space (microsites) and time within a *M. guttatus* population has recently been shown by Mojica *et al.* (2012). Their study examining variation in flower size QTL, found that flower size differs within the population between growing seasons (years) and microsites, as a result of antagonistic pleiotropy with flowering time. Understanding this heterogeneous variation is important to understanding how plants' flowering phenology may change within seasons as a response to changes in their environment.

Evolution under changing climates. Our research can shed light on some of the consequences of a shift in the growing season due to climate change. Early season environment plays a major role in flowering phenology and population structure (Rathcke and Lacey 1985; Hendry and Day 2005). In a warming environment where spring shifts earlier and plants begin to grow earlier, plants will be experiencing shorter photoperiods for longer periods of time. There are several potential outcomes to this. There may be selection favoring the families that have a lower critical photoperiod and flower earlier. This would result in a population that shifts towards an overall earlier flowering time, and reduced clonal growth. This would mimic the pattern of selection that likely produced the annual ecotype of *M. guttatus* (Hall and Willis 2006). Alternatively, the shift in climate may result in plants that grow vegetatively for longer and invest more in clonal growth because they are spending more time in shorter photoperiods and not receiving their critical photoperiod until later in the growing season. Furthermore, as we found in our study, phenotypic selection may be constrained due to negative genetic covariances between traits. These scenarios may ultimately lead to changes in population structure and flowering phenology. Changes in early spring phenology, and the timing of major life history events like bud dormancy, tuber formation, spring leafing, and flowering, as a result of a warming climate have been well

documented (Fitter and Fitter 2002; Parmesan and Yohe 2003; Menzel *et al.* 2006). For example, Memmott *et al.* (2007) investigated the effect of climate change on the interactions between plants and their pollinators, and found that increased atmospheric CO_2 led to phenological shifts and reduced overlap between plants and their pollinators. Ultimately, they suggest that these reduced interactions may result in extinction of both plants and pollinators. A study by Anderson *et al.* (2012) found that earlier snow melt as a result of warming temperatures affected the phonologies in *Boechera stricta* via strong directional selection for early flowering. They found that shifts in flowering time reduce the flower resources available to pollinators. Ultimately, long-term population growth and survival will depend on adaptive genetic evolution, and the ability of plants to integrate environmental cues such as daylength, light level, temperature and water availability to determine the optimal time to transition between life stages.

Genetic components for response to daylength. We detected a significant genotype x environment interaction for biomass allocation (family x treatment, Table 2C). This suggests that selection may favor different genotypes at different points in the growing season. Biomass allocation is one indication of how plants are partitioning their resources. If they have a higher primary branch axis biomass, they are partitioning resources towards sexual reproduction. If they have a higher stolon biomass, they are partitioning resources towards asexual reproduction. To understand how selection might maintain genotypes that have different relative allocation patterns, one would need to assess the fitness contribution of seed versus stolons. Such a study would require multi-year field experiments that realistically determine how recruitment from seed competes with stolon rosettes. In some species clonal reproduction has been found to lead to higher population growth compared to sexual reproduction (Schulze *et al.* 2012), although other

studies show the two reproductive modes of equal importance in some species (Weppler *et al.* 2006). It is likely that the relative importance of the two strategies changes under different environmental conditions in both time and space, as has been found for populations along an elevational gradient (Chen *et al*. 2015).

As predicted by life history theory (Iwasa and Cohen 1989), a trade-off exists between vegetative and reproductive growth in this population. The significant negative genetic correlation between flower number and stolon number might suggest that plants cannot simultaneously allocate resources towards sexual and asexual reproductive growth. Previous work showing shared QTL between flowering time and stolons in an annual x perennial mapping population provide support for this hypothesis (Friedman *et al*. 2015). However, we cannot rule out an alternative explanation that the trade-off could show that families are relatively specialized in either sexual or clonal growth (although in our experiment, all families reproduced via both strategies). The fact that heritable variation in allocation patterns exists suggests that these two reproductive strategies may not result form an inherent constraint in allocation, but rather are an outcome of selection. Although allocation trade-offs between vegetative and sexual reproduction have been well documented in various clonal plant species (Geber *et al*. 1992; Worley and Harder 1996; Ronsheim and Bever 2000; van Kleunen *et al*. 2003), it can be challenging to interpret the mechanism underlying the phenotypic or genetic correlations.

Although it is not possible to assess fitness in a growth chamber study like ours, we are able to interpret the fitness consequences of sexual reproduction using total flower number as a proxy for fitness through sexual reproduction. In our experiment, regardless of daylength, plants that flower early have a greater number of flowers overall (Table 1). This suggests that individuals that flower early have higher sexual fitness over a single growing season. However,

the individuals that are flowering later are investing more towards stolon production (Table 1), and given that this population is perennial, these individuals will likely have higher fitness in subsequent growing seasons. In a recent study by Herben *et al.* (2015), they found that clonality reduced reproductive output (seed number and size), but that clonal individuals also had reduced mortality. Additionally, late flowering individuals that are investing in stolons may out-compete new germinants in future growing seasons. Eckert *et al.* (1999) found that sexual reproduction was greatly reduced, or sometimes lost, in populations of an aquatic plant as a result of environmental conditions not conducive to sexual reproduction. This has led to populations that are exclusively clonal.

Conclusions. We performed a greenhouse experiment to quantify the standing phenotypic variation in a single population of *M. guttatus*, followed by a growth chamber experiment to investigate whether this population exhibits genetic variation and phenotypic plasticity in response to daylength in the timing of growth and flowering. We found that this population is phenotypically plastic and exhibits a trade-off between reproductive and clonal growth. We suggest that the mechanisms maintaining the variation within this single population include genotype x environment interaction, heterogeneous selection over space and time, and negative genetic correlations between traits. Ultimately, this study has shed light on the maintenance of genetic variation in a single population and confirmed the critical role that photoperiod has on flowering phenology. Follow up experiments in the field should be conducted in order to confirm our findings in more natural environments and determine the way selection is maintaining the variation in sexual and clonal strategies.

Table 1. Phenotypic correlations of flowering traits, vegetative growth traits, and biomass for A) 13-hour treatment (n=190, flowering time n=39); B) 14-hour treatment (n=190, flowering time n=107); C) 15-hour treatment (n=190, flowering time n=158) for *Mimulus guttatus* plants grown in growth chambers. *P*-values are shown in parentheses, with bold indicating statistical significance.

	Total flower number	Leaf length (week 2)	Stolon number	Stolon mass	Primary axis mass
A. 13-hour treatment					
Flowering time (days)	-0.69(<**0.0001**)	-0.34 (**0.03**)	0.66 (<**.0001**)	0.47 (**0.003**)	-0.49(**0.001**)
Total flower number		0.24 (**0.001**)	-0.32 (<**.0001**)	-0.34 (<**.0001**)	0.58 (<**.0001**)
Leaf length (week 2)			-0.02 (0.76)	0.05 (0.48)	0.13 (0.08)
Stolon number				0.42 (<**.0001**)	-0.02 (0.80)
Stolon mass					-0.34 (<**.0001**)
B. 14-hour treatment					
Flowering time (days)	-0.62 (<**.0001**)	-0.33 (**0.0006**)	0.71 (<**.0001**)	0.72 (<**.0001**)	-0.23 (**0.02**)
Total flower number		0.28 (**0.0001**)	-0.50 (<**.0001**)	-0.68 (<**.0001**)	0.67 (<**.0001**)
Leaf length (week 2)			-0.14 (**0.06**)	-0.14 (0.05)	0.16 (**0.03**)
Stolon number				0.72 (<**.0001**)	-0.22 (**0.002**)
Stolon mass					-0.43 (<**.0001**)
C. 15-hour treatment					
Flowering time (days)	-0.58 (<**.0001**)	-0.23 (**0.003**)	0.58 (<**.0001**)	0.58 (<**.0001**)	-0.20 (**0.01**)
Total flower number		0.26 (**0.0003**)	-0.49 (<**.0001**)	-0.47 (<**.0001**)	0.56 (<**.0001**)
Leaf length (week 2)			-0.14 (0.05)	-0.13 (0.06)	0.13 (0.08)
Stolon number				0.59 (<**.0001**)	-0.27 (**0.0002**)
Stolon mass					-0.33 (<**.0001**)

Table 2. Summary of REML mixed effect models for fixed and random effects on morphological traits. A) Shows effects on flowering traits, B) shows vegetative growth traits, and C) shows biomass allocation. Bold *P*-values indicate significance.

A.	**Flowering time (days)**		**Total flower number**	
Fixed effects	*F* stat	*P*-value	*F* stat	*P*-value
Treatment	$28.93_{2,18.7}$	**<.0001**	$16.11_{2,19.7}$	**<.0001**
Random effects	*Z* stat	*P*-value	*Z* stat	*P*-value
Family	2.62	**0.004**	2.44	**0.007**
Family*Treatment	1.01	0.16	0.66	0.26
Block(Treatment)	1.44	0.07	0.5	0.31

B.	**Leaf length (week 2)**		**Stolon number**	
Fixed effects	*F* stat	*P*-value	*F* stat	*P*-value
Treatment	$12.27_{2,14.5}$	**0.0008**	$116.47_{2,16.4}$	**<.0001**
Random effects	*Z* stat	*P*-value	*Z* stat	*P*-value
Family	2.86	**0.002**	2.43	**0.008**
Family*Treatment	0.38	0.35	1.13	0.13
Block(Treatment)	1.52	0.064	0.68	0.25

C.	**Stolon mass**		**Branch mass**		**Primary axis mass**	
Fixed effects	*F* stat	*P*-value	*F* stat	*P*-value	*F* stat	*P*-value
Treatment	$27.32_{2,32.1}$	**<.0001**	$12.69_{2,36}$	**<.0001**	$10.76_{2,29.2}$	**0.0003**
Random effects	*Z* stat	*P*-value	*Z* stat	*P*-value	*Z* stat	*P*-value
Family	2.06	**0.02**	2.4	**0.008**	2.48	**0.007**
Family*Treatment	3.1	**0.001**	2.89	**0.002**	2.77	**0.003**
Block(Treatment)	0.73	0.23	.	.	0.98	0.16

Table 3. Pairwise family genetic correlations (r_G) between flowering traits, vegetative growth traits, and biomass allocation for three daylength treatments in growth chambers. Raw *P*-values are presented, and bolded values indicate those that remain significant after Bonferonni correction.

Pairwise trait	**Treatment (daylength hours)**		
	13	14	15
Leaf length (week 2)-Flowering time (days)	-0.6088 (0.006)	-0.6091 (0.006)	-0.4731 (0.03)
Stolon mass-Branch and primary axis mass	-0.4209 (0.08)	-0.2257 (0.40)	-0.1275 (0.62)
Total flower number-Flowering time (days)	-0.8131 (**<.0001**)	-0.9505 (**<.0001**)	-0.9404 (**<.0001**)
Total flower number-Stolon number	-0.9740 (**<.0001**)	-0.7748 (**<.0001**)	-0.7696 (**<.0001**)

Table 4. Genetic variance (V_G), environmental variance (V_E) and broad-sense estimates of heritability (H^2) for flowering traits, vegetative growth traits, and biomass allocation within each growth chamber treatment.

Trait	Treatment	V_G	V_E	H^2
Flowering time (days)	13	426.12	67.21	0.86
	14	155.06	148.91	0.51
	15	139.93	74.93	0.65
Total flower number	13	94.55	65.71	0.59
	14	212.34	141.3	0.60
	15	288.92	129.03	0.69
Leaf length (week 2)	13	0.18	0.12	0.61
	14	0.24	0.16	0.59
	15	0.19	0.14	0.58
Stolon number	13	0.64	2.77	0.19
	14	1.26	1.43	0.46
	15	0.61	0.99	0.37
Stolon mass	13	0.06	0.06	0.48
	14	0.09	0.09	0.50
	15	0.07	0.04	0.62
Branch and primary axis mass	13	0.01	0.009	0.51
	14	0.09	0.06	0.62
	15	0.09	0.03	0.75

Table 5. Summary of REML mixed effect models for fixed and random effects on growth rate traits. Bold *P*-values indicate significance.

	Leaf length (cm)		Leaf number		Stolon number	
Fixed effects	*F* stat	*P*-value	*F* stat	*P*-value	*F* stat	*P*-value
Treatment	$8.57_{2,81.8}$	**<.0001**	$14.19_{2,521}$	**<.0001**	$19.14_{2,1016}$	**<.0001**
Time	$3461.52_{1,1706}$	**<.0001**	$471.29_{1,1649}$	**<.0001**	$1222.38_{1,1704}$	**<.0001**
Time^2	$2047.01_{1,1706}$	**0.0003**	$54.72_{1,1653}$	**<.0001**	$665.49_{1,1704}$	**<.0001**
Time*Treatment	$20.93_{2,1706}$	**<.0001**	$22.40_{2,1649}$	**<.0001**	$20.56_{2,1704}$	**<.0001**
Time^2*Treatment	.	**.**	$6.56_{2,1654}$	0.0014	$7.1_{2,1704}$	**0.0009**
Random effects	*Z* stat	*P*-value	*Z* stat	*P*-value	*Z* stat	*P*-value
Family	2.28	**0.01**	2.39	**0.009**	2.05	**0.02**
Family*Treatment	3.26	**0.0006**	3.08	**0.001**	2.79	**0.0026**
Block (Treatment)	0.38	0.35	0.96	0.17	.	.

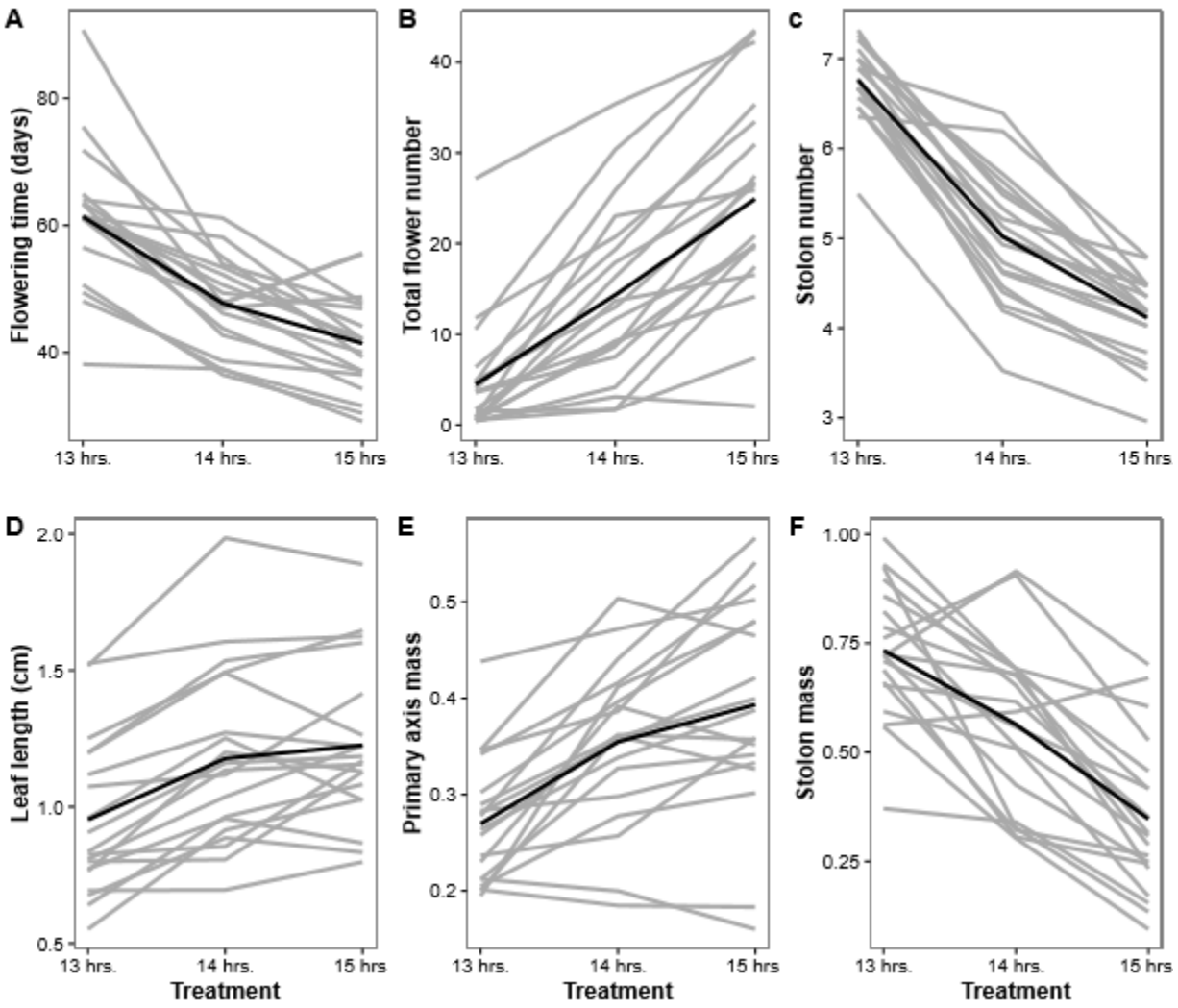

Figure 1. Plasticity in six flowering and vegetative traits for three growth chamber treatments that differ in daylength. Grey lines represent norms of reaction for 19 maternal families, whereas the black line indicates the mean trait values across the 19 families. Families and treatments differed significantly from one another for all traits (Table 2), and the effect of family × treatment is significant for primary axis mass and stolon mass.

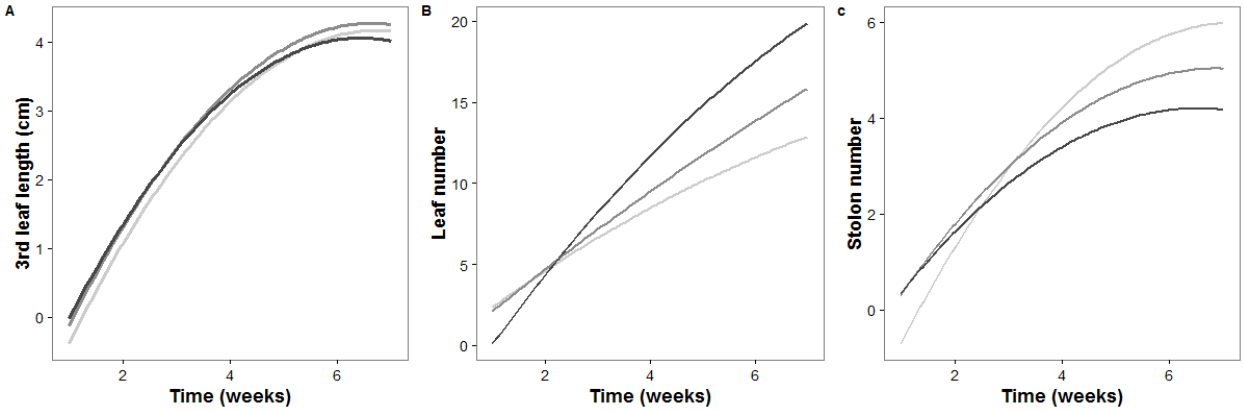

Figure 2. Relationship between vegetative growth and time for A) the length of the third leaf; B) total number of leaves; and C) total number of stolons in three growth chamber treatments. The y-axis values are adjusted for other variables in the model (see Methods). The fitted lines depict quadratic regressions based on a repeated-measures random regression analysis for four sampling times. The light grey line is the 13-hour treatment, the intermediate grey line is the 14-hour treatment, and the dark grey line is the 15-hour treatment.

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EDUCATION

August 2014-August 2016

Master of Science – Biology, GPA: 3.50/4.00
Syracuse University, College of Arts and Sciences, Syracuse, NY

September 2009-May 2013

Bachelor of Science – Biological Science, GPA: 3.46/4.00, Cum Laude
Rowan University, College of Science and Mathematics, Glassboro, NJ

RESEARCH EXPERIENCE

August 2014-August 2016

Master's Research
The effects of genetic and environmental variation on growth and flowering
Advisor: J. Friedman
Investigating the effect of photoperiod on flowering time and growth in a single population of *M.guttatus* that exhibits phenotypic variability.

January-May 2013

Independent Undergraduate Lab/Field Research
Herbivory and plant defense mechanisms: Glucosinolate production response in two *Brassica* species
Advisor: T. Scott
Studied the relationships between herbivory, phytochemical production, and resource allocation.

September-December 2012

Semester-long Undergraduate Research Project (Botany)
Herbivory and phytochemistry: Glucosinolate production in *Brassica rapa*
Advisor: T. Scott

January-May 2012

Semester-long Undergraduate Research Project (Bio IV – Global Ecology)
Habitat variation and its effect on foraging behavior of some winter bird communities of southern New Jersey
Advisor: P. Crumrine

TEACHING EXPERIENCE

August 2014-May 2016

Teaching assistant
General Biology, BIO121 & BIO124
Taught two lab sections (48 students) per semester (3 semesters); requiring small class instruction, grading course materials, developing new quizzes, mentor students as necessary.
Ecology and Evolution, BIO345
Conducted 2 small in-class review sessions before each of the 4 exams, mentored students as necessary, graded course materials.

Genetics, BIO326
Proctored 4 exams

CONFERENCES & POSTERS/PRESENTATIONS

K. Schmid and J. Friedman. Intra-population genetic variation for flowering and growth in response to photoperiod. Talk at The Evolution Conference. Austin, TX. June, 2016.

K. Schmid and J. Friedman. Effects of different environments on allocation strategies in plants. Talk at Biology Graduate Student Seminar Series. Syracuse, NY. April, 2015.

K. Schmid and J. Friedman. Effects of different environments on allocation strategies in plants. Poster at GSO Graduate Student Research Symposium. Syracuse, NY. March, 2015. (Best poster award)

K. Schmid, W. Hurley-Rioux, T. Scott. Herbivory and plant defense mechanisms: Glucosinolate production response in two *Brassica* species. Poster at Ecological Society of America Mid-Atlantic Chapter Meeting. Dover, DE. April, 2013.

K. Schmid, W. Hurley-Rioux, T. Scott. Herbivory and plant defense mechanisms: Glucosinolate production response in two *Brassica* species. Poster at Saint Joseph's Sigma Xi Research Symposium. Philadelphia, PA. April, 2013.

K. Schmid, W. Hurley-Rioux, T. Scott. Herbivory and plant defense mechanisms: Glucosinolate production response in two *Brassica* species. Poster at Rowan University STEM Symposium, Glassboro, NJ. April, 2013.

PROFESSIONAL ACTIVITIES

May 2016
- GSO Travel Award
- Biology Travel Award

April 2016
- Evo-Day 1-day symposium at Cornell University

August 2014-May 2016
- Plant Ecology and Evolution reading/journal group
- Center for Reproductive Evolution meeting

January 2015-August 2015
- Mentored undergraduates (Jeff Darkwa and Anna Bjarvin) who assisted in my research

January 2016
- WISE Scientific Writing Workshop

January-May 2013
- Biology tutor

August 2011-May 2013
- Rowan University Biology Club

SOCIETY MEMBERSHIP

Society for the Study of Evolution
Botanical Society of America