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Small-scale variation in growing season length affects size structure of scarlet monkeyflower

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Growing season length can control plant size over altitudinal and biogeographic scales, but its effect at the scale of meters is largely unexplored. Within the riparian zone of a northern California river, scarlet monkeyflower, *Mimulus cardinalis*, grows significantly larger at sites high in the channel as compared to sites low in the channel, and even larger where tributaries meet the main stem of the river. We explored the hypothesis that markedly different growing season length controls this size variation. Due to the very gradual retreat of the water level following winter flooding, emergence time is three months longer for plants growing at tributary confluences than for plants growing at low elevations in the channel. Consistent with the growing season length hypothesis, we found no difference in transplant growth between river and tributary confluence sites in an experiment where we equalized growing season length at these locations. Moreover, a second experiment showed that individuals planted earlier in the year gain a distinct size advantage over those planted later, even though growing conditions are less ideal. These results suggest that emergence time may be a key determinant of plant size structure along rivers, an important result considering forecasted variation in water flows with climate change.

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All organisms must contend with seasonality, which affects the timing of important life history events. In plants, growing season length affects the amount of nutrients that can be acquired, and how much light and carbon are available for photosynthesis. This in turn influences allocation of energy to growth, defense, and reproduction. The timing of emergence and flowering has been shown to be important for plant success and fitness in both the parent and its resulting offspring (Baskin and Baskin 1972, Lacey and Pace 1983, Galen and Stanton 1991, Kelly and Levin 1997). Plant size may also affect fitness in many plants via a strong correlation between size and fecundity (reference 126: in Roff 1992). Not surprising then, are concerns related to how changing climate will influence plant populations through its effects on growing season length (Post et al. 2001). For example, research in alpine meadows has shown that reduction of snow pack by physical snow removal (Galen and Stanton 1995) or experimental warming (Price and Waser 1998, Kudo et al. 1999) causes plants to flower earlier. A better understanding of the importance of growing season length to population level patterns is essential for forecasting population level responses to climate change.

Rivers with seasonal discharge regimes provide ideal systems for studying the effect of growing season length on size structure over small spatial scales, because the time plants emerge from high flows is controlled by their

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vertical elevation relative to the channel. Thus, plants separated in elevation by one meter may have growing seasons that differ in length by two or three months. As an extreme example, in wide flood plains in the Netherlands, a separation of one cm in elevation changes emergence time by a month (van der Sman et al. 1992). This translates to larger *Rumex maritimus* plants with significantly greater seed output at the end of the growing season (van der Sman et al. 1992). Similar small-scale variation exists in vernal pool and alpine systems, where it has been demonstrated that plants emerging earlier in the season tend to grow larger and have higher fitness than those emerging later (Linhart 1974, Galen and Stanton 1993). Whether these experimentally derived patterns can be applied to other habitats and locations remains to be determined. However, beyond these few studies, the influence of local scale variation in growing season length is largely unexplored. Some studies have examined how variations in snow pack depth and emergence date among years (Billings and Bliss 1959, Walker et al. 1994, 1995, Inouye et al. 2002) or location within a sand dune (Keddy 1982, Martínez and Moreno-Casasola 1993) affects flowering and growth. However, most evidence comes from comparative studies over biogeographic and altitudinal scales (Clausen et al. 1940, Bliss 1956, Ward 1969, Shaver et al. 1986, Kudo 1992). In comparison to competition, herbivory, or physiological stresses, growing season length is rarely considered as an explanation for variation in plant size over the scale of meters.

Despite rivers being ideal systems to study small scale variation in growing season length, they have very rarely been studied. We explored the effects of growing season length on the size structure of scarlet monkeyflower, *Mimulus cardinalis*, along a northern California river. Because of the region's Mediterranean climate, rainfall events beginning in November raise winter base flow above the height of the vegetation in the river channel. During this period, all above-ground stems are removed from *Mimulus* plants, and they persist submerged as rhizomes embedded in stable sedge tussocks (Levine 2000). As the rains begin to cease in spring, flow drops, and plants emerge from winter flows according to their elevation in the channel.

Because of the geomorphology of the Eel River, its tributaries enter the main stem as cascades. *Mimulus* individuals living at high elevations at these confluence sites with the channel, but fed water throughout the year from the smaller tributary cascades, are the first to emerge, typically in March. As flows continue to recede, individuals on high sedge tussocks in the channel, but not at tributary confluences, are the next to emerge, typically in late April. Lastly, individuals living on low sedge tussocks emerge in late May. Since plant growth stops at the end of September (Levine 2000), plants just meters apart experience growing season lengths ranging in length from four to seven months.

In this paper, we test the hypothesis that growing season length causally explains much of the local variation in *Mimulus* size structure. We first demonstrate that the size of *Mimulus* individuals varies in a matter correlated with their date of emergence. We then present the results from two complementary experiments, one where we experimentally equalized growing season length across habitats, and another where growing season length varied naturally among locations.

Methods

Study system

The scarlet monkeyflower, *Mimulus cardinalis*, is a common species along the South Fork Eel River in northern California (39°44′N, 123°39′W). Fieldwork was conducted at all riffle (14) and tributary confluence (7) sites along an 8 km stretch of the river. *Mimulus* has bisexual red, tubular flowers that are primarily hummingbird-pollinated, but this species can also asexually reproduce through rhizomes (Sutherland and Vickery 1988). In the channel of the South Fork Eel, *Mimulus* grows mainly on the sediments trapped within tussocks formed by the sedge *Carex nudata*. These tussocks, which grow predominantly in riffles, provide a stable habitat in the constantly shifting riverbed for most riparian species, including forbs, grasses, mosses, and liverworts. Although *Carex* competes with the species growing on its tussocks, limiting their size, their winter survival is significantly increased on tussocks compared to plants growing on the riverbed (Levine 2000). During winter floods, tussocks are completely submerged, shoots of all the forbs die, and most plants survive the winter by storing energy in rhizomes. Only after the water subsides, and the plants emerge from winter flows, does *Mimulus* begin growing back from rhizomes. Seedling establishment is very low (Levine 2000).

Documenting natural patterns

Mimulus growing in tributary confluence cascades emerge from winter flows two to three months before plants growing in the main channel of the Eel river due to their higher elevation. To quantify the size difference between plants at tributary confluence cascades and those in the main channel, we randomly selected five plants at each of the fourteen riffles along the Eel, and at each of the confluences of the seven tributaries in late summer 1999 (not all locations contained five plants; Eel: $N = 68$; tributary: $N = 25$). Riffles were delimited by water flow in the channel and the presence of *Carex nudata,* and averaged 20 m in length. Only *Mimulus* growing directly on the edge of either side of the channel were included in the analysis. As a measure of size, we counted all leaf pairs (log leaf number is highly correlated with biomass; $R^2 = 0.67$, $P < 0.001$), and the five plants per site were averaged for analysis. To document how the size of plants growing within the main channel relates to their elevation above the water level, changing emergence times up to a month, we counted leaf number for all *Mimulus* plants growing directly along the edge of the channel at each of the fourteen riffle sites ($N = 67$). For each plant, we also measured the vertical distance from base of the plant to the river to get a relative measure of elevation in the channel.

Experimentally equalizing growing season length

If the differences in plant size amongst the various Eel habitats are controlled by varying growing season lengths, then these differences should disappear when growing season length is experimentally equalized. That is, given the same amount of time to grow, plants should achieve a similar size. If they do not, this indicates that other intrinsic features of the locations, such as nutrient or water availability, are important. For example, competition with *Carex* might also contribute to the smaller size of *Mimulus* on low tussocks; sedge tussocks growing low in the channel tend to be more robust due to higher water availability (J. Williams and J. Levine, pers. obs.).

To determine whether size differences within the river were controlled by differences in non-phenological aspects of habitat quality or alternatively, by differences in growing season length, we transplanted equal-sized plants onto eight high and low elevation tussocks at each of four different sites in early June 1999 ($N = 32$). High elevation tussocks typically emerge from winter flows in late May, one month before low elevation tussocks. A high elevation tussock was defined as a tussock at least 30 cm out of the water, and a low tussock as one that was less than 5 cm out of the water. All tussocks had emerged from the water at the time of initial transplanting. Due to the clonal nature of *Mimulus*, we could very easily locate similar sized ramets at each site with three to four leaf pairs and similar sized rhizomes. Transplants were taken from the site in which they were planted. Half the plants were randomly assigned to a sedge clipping treatment to test the possibility that sedge above-ground competition differentially impacted high and low plants. Specifically, the surrounding sedge stems were clipped to soil level on half of the high, and half of the low tussocks for the duration of the experiment.

Plants were allowed equal length growing seasons of four months, from initial transplant date in early June until September 1999. We estimated above-ground biomass in September by counting node number (the number of leaf pairs), maximum leaf length, and plant height. A previous experiment showed that above-ground growth of first-year transplants ceased by the end of August (Levine 2000), so early September was determined to be an adequate cut-off to measure above-ground plant size at the end of the growing season. The location of all plants was marked with small metal stakes and their survival through the winter of 1999-2000 was assessed the following spring. Above-ground dry weight was assessed at the end of the growing season in 2000 when plants were collected. Biomass was estimated from a regression using the non-destructively measured characters as dependent variables from all transplants in the study ($\ln(\text{biomass}) = -3.843 + 0.045 \times (\text{node number}) + 0.180 \times (\text{leaf length}) + 0.056 \times (\text{height})$; $R^2 = 0.81$, $N = 98$). The estimated log biomass from the first growing season was used for all analyses to meet ANOVA assumptions of constant variance. We also measured soil water content in 1999 by weight of water in small soil plugs taken from each tussock.

River vs tributary confluence comparison

As an alternative to the two to three month head start in emergence time of tributary confluence plants, size differences between tributary confluence plants and those at lower elevations in the main channel may be driven by the fact that nutrient availability in the water of small streams may be higher than that of rivers with more open canopies (Vannote et al. 1980). Considering that *Mimulus* growing at confluences are fed with stream water for most of the growing season, variation in nutrient availability may be responsible for the larger size of plants growing at tributary confluences. To distinguish this hypothesis from that involving growing season length, we again equalized growing season length. We grew two plants of equal size (6 leaf pairs, on average, with equal-sized rhizomes) at the confluences of each of seven tributaries that enter the Eel River and at a paired site in the Eel approximately 50 m upstream of each tributary ($N = 28$). However, to ensure that we accurately tested the water quality effect, we grew these plants hydroponically by attaching them with wire to steel cylinders (diameter = 1.2 cm) hammered into the streambed. Plant height was adjusted weekly as water levels dropped. At each site, one *Mimulus* transplant came from a plant in the Eel and the other from a plant in the tributary to ensure that any genetic differences between channel and tributary would not influence the results; transplant origin was not included in the analysis. All plants were started growing hydroponically at the beginning of June, and in September, at the end of the growing season, plants were collected from the rebar and their above-ground dry weight was assessed. Biomass was log transformed to meet ANOVA assumptions of constant variance.

Variable growing season length experiment

To further test whether the additional month(s) of emergence are advantageous for plant growth, we initiated an experiment in 2000 where we allowed growing season length to vary between elevations by starting transplants when sites at each elevation emerged from the river. If we were able to replicate the natural pattern of larger plants at higher elevations in the river when they were started at equal sizes, that would be further evidence to support the growing season length hypothesis. Alternatively, if transplants given a head start did not attain a larger size due to poor early season growing conditions, then another explanation would be needed to explain the pattern. Transplants were planted at three elevations in the river: tributary confluences in March, high tussocks in early May, and low tussocks in early June, allowing growing season length to vary from three to six months, similar to the natural variation in growing season length. Five transplants of the same size (3 or 4 leaf pairs and equal-sized rhizomes) were started at each of four sites at the three elevations in the river. Although having only four sites reduced our ability to detect small differences in plant size, we chose all available sites along an 8 km stretch of river that included a tributary and riffle area in close proximity. Above-ground biomass was estimated at all sites in mid-June and late July using the same regression described in the first transplant experiment. In late August 2000, plants were collected and above-ground biomass assessed. Final biomass was log-transformed for the analysis to meet ANOVA assumptions of constant variance. The mean log biomass at each site and elevation combination was used in the analysis to avoid pseudoreplication. This experiment allowed us to test whether the early emergence at higher sites could translate into larger plants.

Results

Growing season length of *Mimulus cardinalis* ranged naturally from four to seven months, with plants emerging at tributary confluence cascades in March, at high elevation tussocks in the main channel in April and at low elevation tussocks in the main channel in May. In our analysis of natural patterns, *Mimulus* growing at tributary confluences were six times as large as plants growing in the Eel River (Fig. 1, $F_{1,18} = 29.11$, $P < 0.001$). Furthermore, within the main channel, plant size was positively correlated with elevation of its base above the stream surface (Fig. 2, $R^2 = 0.25$, $P < 0.001$).

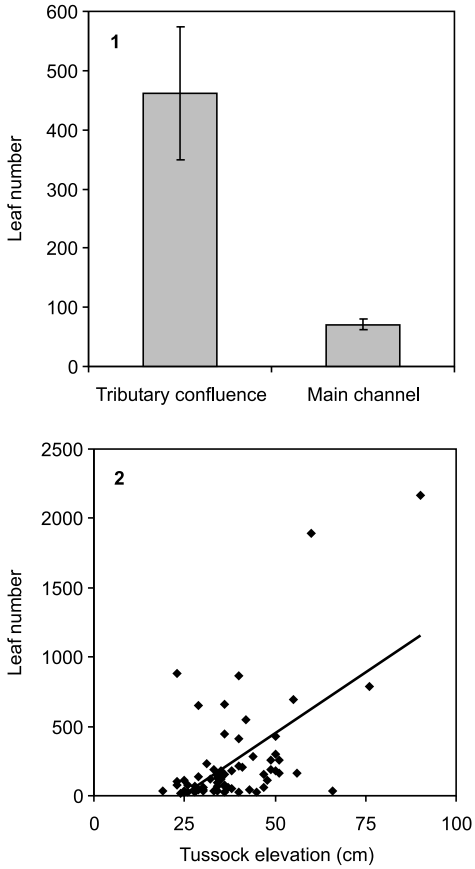

Fig. 1–2. Natural patterns. (1) Size of *Mimulus* at tributary confluences and at riffles in the main channel, measured as leaf number. Error bars show ± 1 se. (2) Correlation between the size of *Mimulus* growing in the main channel, and the elevation of the base of the plant relative to summer base flow.

Consistent with the growing season length hypothesis, when growing season was equalized, plants on high elevation tussocks were not larger than those on low tussocks. In fact, the reverse was true. *Mimulus* on low elevation tussocks were twice as big as those on high tussocks (Table 1, Fig. 3). This may be explained by the higher soil water availability in low (mean ± se = 31.8 ± 2.4%) vs high (17.9 ± 1.5%) sedge tussocks ($t_{30} = 4.95$, $P < 0.001$). Plant size was not significantly impacted by clipping neighboring sedges (clipped: mean ± se = 0.17 ± 0.046 g, unclipped: 0.12 ± 0.037 g; Table 1). During the period of submergence, however, the relative advantages of low and high tussocks were different. Less than half of the transplants on low tussocks survived winter floods compared to three-quarters of those growing on high tussocks, but this difference was not statistically significant ($\chi^2_1 = 3.24$, $P = 0.072$).

When growing season length was equalized across the river and tributary confluence locations for plants grown

Table 1. Summary of ANOVA for transplant experiment on high and low tussocks within the river channel: effects of tussock elevation and decreased competition with sedge tussocks via a clipping treatment on plant size measured as estimated above-ground biomass at the end of the first growing season.

Source of variation	df	F	P
Site	3	6.795	0.002
Tussock elevation (high or low)	1	8.345	0.008
Clipping treatment	1	3.841	0.074
Clipping × elevation interaction	1	0.135	0.716
Error	25		

hydroponically, the tributary individuals were no larger than those grown in the river (Fig. 4, Location $F_{1,18} = 0.004$, $P = 0.98$). When transplants were out-planted at the natural time of emergence in the different river habitats, plants placed at tributary confluences attained much larger size than their river counterparts, though plants on high tussocks were similar in size to those on low tussocks (Fig. 5, $F_{2,9} = 3.73$, $P = 0.066$). The only marginally statistical significance of this result, despite large differences between Eel and tributary confluence plants, stems from the small number of available sites, and thus sample size ($N = 4$). A posthoc power analysis demonstrated that to achieve significance with the same effect, we would have needed to include six or greater replicate sites. However, only four were available that met our criteria.

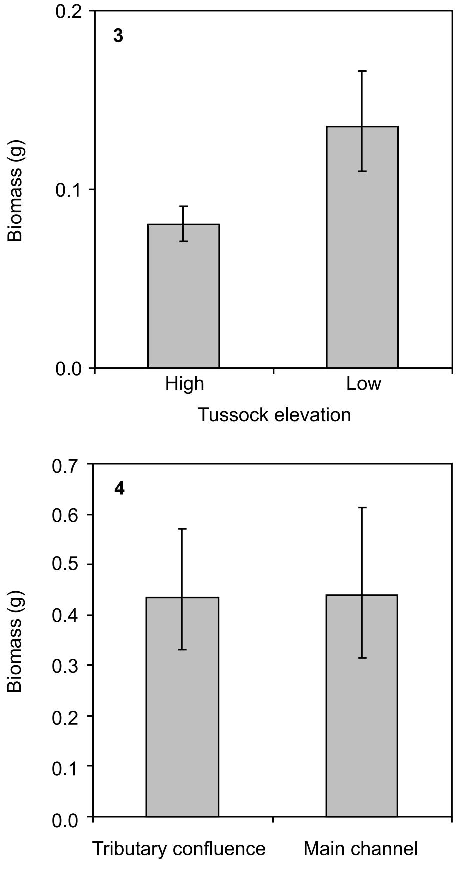

Fig. 3–4. Results from transplant experiments equalizing growing season length. (3) Plants on high and low elevation sedge tussocks within the main channel. (4) Plants grown hydroponically within the channel or at tributary confluences. Data reported are back-transformed means and ±1 se from the log above-ground biomass used in analyses.

Discussion

Our study shows that growing season length is a primary determinant of the six-fold size differences between *Mimulus cardinalis* plants growing in the channel of the Eel River and those grown at tributary confluences within the study area. When transplants were given a two-month head start at sites in tributary confluences, they grew significantly larger than plants growing in the main channel (Fig. 5), yet when growing season was equalized for plants grown hydroponically, no differences were found (Fig. 4). Even though air temperature is cooler early in the spring when tributary confluences emerge from the water, the two-month head start gives tributary confluence plants a distinct advantage. In alpine and high latitude environments, temperature is a key determinant of germination time and growth rate and thus emerging earlier may not necessarily confer an advantage (Bliss 1985, Walker 1987). However, other studies have demonstrated in alpine systems that plants emerging from the snow earlier can grow larger and have

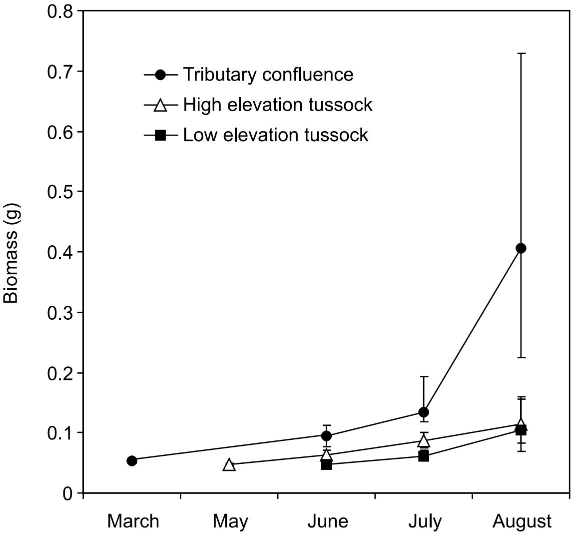

Fig. 5. Results from experiment transplanting equal-sized *Mimulus* individuals to tributary confluences, and high and low elevation tussocks, at the time of habitat emergence. Error bars show ±1 se.

higher fitness (Billings and Bliss 1959, Galen and Stanton 1995, Walker et al. 1995, Price and Waser 1998, Totland and Alatalo 2002).

We also found that growing season length may be important for explaining the positive correlation between *Mimulus* size and its elevation above the channel for plants growing on tussocks in the main channel of the river. However, when we planted individuals at the time of their habitat's emergence from winter flows, plants growing on tussocks higher in the channel did not maintain a size advantage through the season even though they had a month-long head start. In fact, plants grown on low tussocks were able to catch up (Fig. 5), and when started at the same time to equalize growing season length, transplants on low tussocks grew larger (Fig. 3). This pattern is remarkably similar to that found by Keddy (1982), who found that *Cakile edentula* growing near the lakeshore and germinating a month later than those growing landward were much larger. He attributed this to better growing conditions near the lake. *Mimulus* growing on low tussocks may have a similar advantage due to higher water availability throughout the growing season. This is in contrast to plants growing in alpine snow beds where longer growing seasons at the edge of the snow bed are positively correlated with more favorable growing conditions due to higher water and nutrient availability during crucial developmental stages (Galen and Stanton 1995). Yet, the general trend in size variation of naturally occurring plants was that *Mimulus* growing at lower elevations in the river channel were smaller. Winter survivorship data of transplants suggest that stresses associated with submergence may partly explain the smaller size of plants on low tussocks. Although low over-winter survival could be attributed to transplants being pulled out of the tussock more easily than naturally occurring plants, transplants persisting on low tussocks still had poorer survival. Hence, winter flooding may be more important than growing season length in explaining the size difference between high and low plants elevation within our main channel study area.

An additional factor that affected plant size and fitness that became more apparent as the growing season progressed was herbivory by deer and weevils. Deer removed some *Mimulus* stems before and during flowering. Weevils ate leaves on certain plants and their larvae chewed out some meristems, giving attacked plants a shriveled appearance. Still, no differences were found in the proportion of plants attacked on high and low tussocks ($\chi^2_1 = 0.53$, $P = 0.47$). Plants grown hydroponically at sites in the river and tributaries were less affected by weevils, but suffered some herbivory by deer. However, deer did not preferentially eat plants at tributary confluences as compared to those in the channel ($\chi^2_1 = 0.20$, $P = 0.66$). Thus, while herbivory significantly decreased plant size overall, its effects did not vary with elevation in the channel.

Growing season driven size differences may partly explain *Mimulus* abundance patterns. Consistent with a positive correlation between plant size and flower number ($R^2 = 0.696$, $F_{1,66} = 148.56$, $P < 0.001$; J. Levine, unpubl.), the larger plants growing at tributary confluences have a much higher reproductive output than plants growing in the channel (J. Williams, pers. obs.). High local seed dispersal may be responsible for the five-fold greater density observed at tributary confluences (tussock occupancy = 0.34) as compared to riffles in the main stem Eel River (tussock occupancy = 0.07; Mann-Whitney U-test = 5.5, $P < 0.001$). Increased seedling establishment success at tributary confluences may also contribute to these patterns. At a larger scale, the high reproductive output of plants at the confluences may subsidize *Mimulus* populations in the channel, a far less optimal habitat. Channel populations are seed-limited (Levine 2001), and a large proportion of the seed produced in the entire drainage comes from tributary confluences, which compose a very small proportion of the drainage area. Thus, confluence plants are likely acting as propagule sources in the population and channel riffle sites perhaps as sinks. This source–sink dynamic may have important effects on the population structure of *Mimulus* in the Eel River. A similar source–sink dynamic has been observed in a Colorado population of snow buttercup, *Ranunculus adoneus* and in a lake shore plant, *Cakile edentula* (Keddy 1982, Stanton et al. 1997), and may well occur in other systems where growing season length controls phenology.

Our study is one of the few to identify the importance of growing season length as a control over local scale variation in the size structure of a plant population. Several studies have demonstrated that distance from the center of a vernal pool or basin filled with snow is related to plant abundance and performance because of growing season length (Linhart 1974, Galen and Stanton 1993, 1995). In these habitats growing season length is longer in the middle of the patch compared to the periphery due to gradual water evaporation or snowmelt. In some instances, plants separated by only a few meters do not exchange pollen, because the timing of flowering is controlled by snowmelt. Early flowering plants will then act as sources in the population since later flowering plants may not have the time or resources to set seed (Stanton et al. 1997).

In the North Coast range of California where this study was conducted, global climate models predict an increase in total and late season rainfall over the next thirty to fifty years (Field et al. 1999). This increase in winter rainfall will push emergence time further into the summer, because it will take longer for the river height to diminish following winter rains. The results of our experiments lead to the prediction that with increased winter rains, *Mimulus cardinalis* plants will be smaller overall, and because smaller plants produce fewer flowers, reproductive output would decrease. Depending on the importance of colonization events in sustaining population size, abundance and distribution patterns might also change. Given that many riparian plants grow at different elevations in river channels, this pattern might be applicable to other species and rivers. By further understanding how growing season length controls phenology and population structure, we can begin to better predict how climate change will alter this and other river systems.

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