POTENTIAL EFFECTS OF CLIMATE CHANGE ON *PENSTEMON PALMERI* AT ZION NATIONAL PARK, UTAH, U.S.A.

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Abstract

Climate change, whether referring to historic ice ages or contemporary shifts in global climate patterns, has been linked to wide-ranging and regionally variable changes in biotic communities. Environmental shifts predicted for the southwestern United States include increased temperature and aridity, elevated levels of atmospheric CO_2 and increased risk of wildfire. The impacts of these shifts on plant and insect communities on the Colorado Plateau are currently poorly understood. Using elevation as a proxy for climate change, I tested the following hypotheses to increase understanding of the effects of warming on *Penstemon palmeri* (Plantaginaceae): 1) At lower elevations and higher temperatures, *P. palmeri* has greater vegetative and reproductive productivity; and 2) Pollinator community composition for *P. palmeri* differs along an elevation gradient. Data were collected on vegetative and floral phenotype, insect community composition and other environmental characteristics at 10 sites along an elevation gradient in Zion National Park, Utah. An experimental study using two growth chambers simulating current mean springtime temperatures and forecasted springtime temperatures for the year 2050 was conducted to assess direct effects of warming on plant phenotype. *P. palmeri* individuals at low elevations produced more, taller stems per plant, more above- and below-ground biomass, larger fruits, and seeds that germinate more quickly than populations at higher elevations. However, corolla tube volume was smallest at low elevations, suggesting differential resource allocation that could be a result of selective pressures from a different pollinator community or other environmental factors. While there was a low germination rate (<0.1%) in the growth chamber experiment, trends in the data suggest seeds from low elevations germinate and leaf out and grow more quickly, and that production of above- and below-ground biomass is greater at higher temperatures and from low elevation seeds. Results from this study provide insight into the future of *P. palmeri* and a springboard for continued research on the effects of climate change on native plants used in restorations and post-fire reseedings.

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Introduction/Background

Climate Change and the Colorado Plateau. Glacial to interglacial environmental shifts have occurred over the past 2.5 million years that have been accompanied by large fluctuations in temperature, CO_2 and precipitation (Davis and Shaw 2001). While many species went extinct during these periods (Barnosky 2008), others were able to survive through adaptation or range shifts (Davis *et al.* 2005). Contemporary climate change is believed to cause poleward-shifting ranges of many biotic communities (Thomas et al. 2001, Parmesan and Yohe 2003). Shifting plant-pollinator interactions due to phenotypic, phenological and range-related changes are understudied (Burkle and Alarcón 2011) but are key elements to understanding how these interactions and resulting plant reproductive success will be affected by climate change (Cleland et al. 2007).

In addition, predicted rates of climate change require plants to adapt at a rapid rate (Huntley *et al.* 1997), given that the rate of contemporary anthropogenic climate change is unprecedented over the past 22,000 years (Joos and Spahni 2008). Climate changes in the past have been cyclical, rather than stochastic (Millar 2006) and ice ages have appeared and subsided in approximately 100,000-year cycles (Shackleton 2000). Projected mean annual temperature increases in the 21st century alone are far greater than what is represented in the natural variability of the past 1,000 years or what the variability since the last interglacial period would have predicted (Crowley 2000). The effects of the current, rapid rate of climate change could be made more unpredictable by temporally mimicking a stochastic event more closely than a cyclical event.

The increase in regional and global temperatures and atmospheric levels of CO_2

associated with current anthropogenic climate change (IPCC 2007) has already had and will continue to have diverse consequences on the seasonal activity associated with plant reproduction (Galen and Stanton 1993, Chapin III et al. 2000, Visser and Holleman 2001, Walther *et al.* 2002, Badeck *et al.* 2004, Visser *et al.* 2003). These consequences can be difficult to predict because they change in space and time, and differentially affect the environment at every scale, from species to ecosystem (Levin 1992, Marshall *et al.* 2008). Predicted climate change can have large effects on plant-pollinator relationships, but there is a paucity of research that explores these effects (Phillips *et al.* 2010), in particular in the southwestern United States, including the Colorado Plateau.

The Colorado Plateau covers approximately 38 million ha of Utah, Colorado, Arizona and New Mexico (Clements 2004) and encompasses a variety of ecosystems including ponderosa pine woodlands, sparsely vegetated piñon-juniper woodlands, shrublands and savannahs, red rock desert ecosystems, high elevation plateaus and isolated mountain peaks (BLM 2009). The elevation within the area ranges from about 610m above sea level at the surface of the Colorado River to nearly 3,660m above sea level in the LaSal and Henry Mountains in Utah (BLM 2009). Habitats in the Colorado Plateau typically exhibit low productivity, which leads to slow recovery after disturbance (Schwinning *et al.* 2008). The lower elevation scrublands have historically experienced low total and highly variable precipitation, low disturbance from fire and grazing and are some of the most sensitive ecosystems to both past and current climate change (Schwinning *et al.* 2008, Vivoni *et al.* 2009). The Colorado Plateau region is especially at risk for unpredictable climatic variation due to its geographical position in the dry interior end of two moisture trajectories (Schwinning *et al.* 2008). The regional climate is predicted to become warmer (IPCC 2007) and experience droughts of greater severity and possibly of greater duration in the future (Seager *et al.* 2007). These factors combined with an increase in revegetation activities on the Colorado Plateau and a lack of both supply and understanding of locally adapted native plant materials for use in restorations (Peppin *et al*. 2010) makes it clear that more research on native plants used in area restorations are valuable to conservation efforts.

Simultaneous with increases in temperature and decreases in humidity within the past century have led to less frequent and less voluminous rainfall (Schwinning *et al.* 2008). Temperature and precipitation differ greatly throughout the semiarid southwest and have highly variable effects at different locations, elevations, and community compositions (Vivoni *et al.* 2009). Warmer temperatures may affect phenology and phenotype of many plant and pollinator species, and their relationships to each other.

If flowers are smaller, less abundant, or less able to produce sufficient advertisements and rewards, pollinators may be less likely to visit them which could result in depressed reproductive success (Willson and Price 1977, Galen 1989). In simulated ecosystems at higher temperatures, more flowers and seeds have been produced in some herbaceous plant species along with greater volumes and concentrations of nectar and scent (Serreze *et al.* 2000, Sabate *et al.* 2002, Hughes 2003). Other studies have found that higher temperatures favor slow-growing, cold-adapted species that germinate earlier in the season (Kimball *et al.* 2009). Patterns of temperature change are important to consider in the examination of ecosystem and species responses to climate change on the Colorado Plateau, especially in light of the increased need for restorations and post-fire reseedings (Colorado Plateau Native Plant Initiative 2009).

Phenotypic shifts in plant traits may result from climate change, including changes in floral morphology (Pritchard *et al.* 1999), scent, color, display size, nectar (Davis 2003), pollen, or oils, all of which are important advertisements or rewards in plant-pollinator relationships (Case and Taper 2000). For example, an increase in ambient CO_2 can cause to a greater carbon-nitrogen (C-N) ratio (Rastetter *et al.* 1992), leading to greater production of secondary compounds in nectar. Phenotypic changes caused by increased CO_2 may also include shifts in composition or volume of plant volatile organic compounds that produce fragrance (Yuan *et al*. 2009). Temperature can also have physiological effects on species (Apple *et al*. 2000, Hou *et al*. 2010, Poroshin *et al*. 2010) and quantifying those effects may prove valuable for both prediction of future patterns and for conservation efforts (Williams *et al*. 2008, Fuller *et al*. 2010).While research has been conducted on some of the phenotypic effects of climate change on plants, much of it has concentrated on crops and grasses (Rastetter *et al.* 1992, Ainsworth *et al.* 2008, Travers *et al.* 2010) rather than on native forbs (non-graminoid flowering herbaceous plant species).

The phenotype of a plant species has the potential to affect mutualisms with pollinators. Most angiosperms experience mutualisms with a few pollinators that are important to their continued fitness (Bond 1994, Waser *et al.* 1996, Kearns *et al.* 1998). Different pollinator communities can also exert differential selective pressures on floral morphology (Pérez-Barrales *et al*. 2007, Sletvold *et al*. 2010), which can effect reproductive success due to the differences in the effectiveness of particular pollinators on flowering species (Sletvold *et al*. 2010). Phenotypic or phenological mismatches between plants and pollinators due to range shifts, warming, or other environmental can be problematic to plant reproductive success. About half of angiosperm species are self-compatible (Igić and Kohn 2006), meaning they can produce viable offspring by self-fertilization with no pollinator present. Some angiosperm species, especially those that are self-incompatible, require effective pollinator visitation for reproduction to occur. While compensatory mechanisms such as vegetative propagation and self-pollination may enable a species to persist in the short term (Bond 1994), plant and pollinator species may not have the capacity to expand their ranges or adapt to environmental change quickly enough to avoid reproductive isolation, inbreeding and potentially inbreeding depression.

Range shifts are a consequence of climate change that has already been documented across many taxa (Parmesan and Yohe 2003, Battisti *et al*. 2005, Beckage *et* al. 2008, Marini *et al*. 2009) and could lead to further changes in phenotype, whether due to genetic variation or phenotypic plasticity. Plants shift their ranges to higher latitudes and elevations in response to warming conditions (Thomas 2010), but not all species respond at the same rate in time or space which can cause phenotypic and trophic mismatches (Schweiger *et al*. 2008, Walther 2010). This means that geographically shifting plants will have to continually respond to new sets of environmental conditions, both in terms of abiotic surroundings and biotic communities. Different plant species may change phenotypically in response to warming, either due to existing genetic variation or plasticity (Nicotra *et al*. 2010).

Elevation is often used as a proxy for warming and climate change because temperatures are higher at low elevations and become cooler at higher elevations (Lookingbill and Urban 2005, Rodeghiero and Cescatti 2005, Gilbert 2010). Pollinator and plant community compositions have been shown to shift along gradients of temperature, affecting their interactions (González *et al*. 2009). Shifts in pollinator community composition along elevation gradient is also associated with changes in floral morphology, as in two hybridizing species of *Penstemon* and the associated pollinator communities up a mountainside (Kimball 2008) and numerous other flowering species (Lavergne *et al.* 2010). Studying how floral morphology shifts with pollinator communities in response to warming in the southwest is important to the development of effective conservation strategies (Burkle and Alarcón 2011).

Research on native plants that might be used for restorations on the Colorado Plateau is especially important as the need to restore these ecosystems has increased over the past several years (Colorado Plateau Native Plant Initiative 2009)**.** *Penstemon palmeri* (A. Gray) is a short-lived perennial forb (Cronquist et al. 1984) with self-incompatible flowers (Walker-Larsen and Harder 2001) that is found in the western United States, often in disturbed areas with dry soils such as washes and roadsides (Kitchen and Meyer 1994) at elevations ranging from 800m-2750m (Kitchen and Meyer 1994). It is primarily bee-pollinated, with occasional bee and wasp nectar robbers (Walker-Larsen and Harder 2001). Due to its status as a native early successional forb that persists after disturbance and serves as wildlife forage (Uncompahgre Project 2008, National Resources Conservation Service 2011) and enhances habitat for pollinators (Ogle et al. 2011), *P. palmeri* is desirable for conservation efforts throughout the Colorado Plateau including restorations and post-fire reseedings (Uncompahgre Project 2008). However, very few empirical studies of *P. palmeri* have been performed and no studies have attempted to test for potential phenotypic shifts and changes in pollinator community in response to climate change. This object of this study is to test the following hypotheses: 1) At lower elevations and higher temperatures, *P. palmeri* has greater vegetative and reproductive productivity; and 2) Pollinator community composition for *P. palmeri* differs along an elevation gradient.

Materials and Methods

Site selection. Eleven sites in Zion National Park were chosen along an elevation gradient ranging from 1352m to 1762m (Fig. 1). Sites were selected to be as accessible and evenly spaced as possible and grouped into low, medium and high elevation categories (Table 1). Due to the nearly continuous distribution of *P. palmeri* individuals along the slope rather than independent populations, the elevation categories were created for clarity of analyses and to reduce the number of post-hoc pairwise tests required to test for differences in individuals between elevations. Differences in both elevation and distance within and between categories were minimized to the extent possible. Sites at each elevation category exhibited the following qualitative environmental differences: low sites were in an area had been recently burned and were located several meters away from a road; medium sites were rocky, close to or on a road, and very windy; and high sites were close to or on a road.

Phenotype. Floral morphology data were collected twice weekly at each site in Zion National Park, Utah from June 14th through July 17th, 2010. Traits were measured (Fig. 2) on 2.8+/-1.2, 1 s.d. haphazardly selected flowers per plant (n=273 total flowers and 24.7+/-12.8, 1 s.d. flowers per site) on 8.9+/-4.6, 1 s.d. focal plants at each site: corolla tube length, two measurements of corolla diameter (corolla diameters 1 and 2), two measurements of anther insertion (distal and proximal to ovary, respectively), staminode length, mouth diameter, upper and lower lip lengths and widths, and distance from anthers to corolla floor. These particular traits were chosen for measurement following measurements for the *Penstemon* genus outlined in Wilson *et al* 2004, modified for *Penstemon palmeri*. All traits were measured to the nearest 0.5mm using a digital caliper. An attempt was made to obtain nectar volume and sucrose levels (as a measure of secondary compound production), but no nectar was present at the time of measurement. Approximate fruit:flower ratios were recorded at each site on a total of 1179 stems on 194 focal plants. Number of stems per plant and all stem heights were recorded on each plant used for floral morphological measurements (n_{stems}=1242 from the same 204 plants used for floral morphology). In early September 2010, fruits from ten plants at ten sites (sites 1-3 and 5-11) were collected haphazardly from each site (not necessarily from the same plants used for other data) and labeled by date, site and a unique identification number. Reproductive success was measured by weighing 10 randomly selected fruits from each of 5 random maternal lines per site. Collected fruits were had not yet dehisced and retained all seeds.

To help account for other environmental differences between sites during analyses, associated species within 5m of focal plants were recorded at eight of the eleven sites.

Pollinator Visitation Rates and Community Composition. Pollinator visitation data was collected through pollinator observations. Start and end time, time of each observed visit and morphospecies of each visitor were recorded. Four to seven pollinator observations (collected by two to three human observers and two to four cameras) were conducted for 20 minutes twice a week at each site for five weeks. Four hundred minutes of observations were collected per week, totaling 2,000 minutes over five weeks (200 minutes per site). On the day of pollinator observations at each site, temperature, relative humidity, precipitation and approximate cloud cover were recorded.

Pollinator community composition was assessed with insect pan traps (3oz Solo cups spray-painted fluorescent yellow, fluorescent blue or white and filled with a solution of water and Ultra Dawn Original Dishwashing Liquid, following LeBuhn et al. 2011) once a week at each site. Four pan traps of each color were set out in the evening and collected the following morning, after approximately 16 hours. Trapped insects were stored in a 70% alcohol solution and brought back to the Chicago Botanic Garden (CBG), Glencoe, Illinois, where they were sorted by morphospecies, identified to the lowest taxonomic level possible (to family for most species), and analyzed by site to test for community differences.

Growth Chamber Experiment. An experiment was conducted using two growth chambers at CBG to test for differences in growth patterns between current and future temperatures and whether differences observed in the field were due to genetic variation or phenotypic plasticity. One growth chamber simulated current mean springtime temperatures in Zion National Park, based on a 30-year dataset (Western Regional Climate Center 2011), and the second growth chamber simulated temperatures projected for the year 2060 (2-4°C higher) based on regional projections for western North America (IPCC 2007). In both chambers the lights were set to mimic actual springtime sunrise and sunset times in Springdale, UT (Edwards 2010). Eighteen seeds were randomly selected from each weighed fruit (see above) and on 30 November 2010 planted three seeds from the same fruit in each of 2800 cells (28-16x30x18cm flats of 200 cells each, Ray Leach “Cone-tainer”™ Single Cell System) in a fully randomized design. Every other cell contained a 12x2.5cm low-density plastic planting tube with UV stabilizers and with a tapered bottom and drainage holes. Germination date, date of first true leaf, and heights of all seedlings were recorded every two to three days, which gave me days to germination from planting, days to first true leaf from germination, and growth rate. Growth rate was calculated by dividing height at time of harvest by the number of growing days. At the same time as data collection, flats were each rotated 180° and shifted one spot clockwise within the growth chamber to avoid placement effects. All flats were bottom-watered every three to four days. The two growth chambers were not identical: chamber A had higher relative humidity than chamber B due to a mechanical issues until it was resolved on day 52; in chamber A flats were placed on the floor with lights lowered to them and in chamber B flats were placed on one tier of a shelving unit with built-in lights. To avoid chamber effects, flats were moved and temperature and lighting regimes were switched between chambers every two weeks.

Seedlings were harvested 75 days after planting and 60 days after the first germination, on 12 February 2011. Shoots were separated from roots using a razor blade, root systems were rinsed of as much soil as possible and dried on paper towels. Each root and shoot system was placed in a separate coin envelope labeled with site and cell information which were then placed overnight in a herbarium specimen dryer cabinet (Lane Science Equipment, NY) at 35.5ºC. Above- and below-ground dry biomass were weighed on a balance (A&D HR-200) the nearest thousandth of a gram.

Because of the low germination rates, tetrazolium chloride assays were performed to test for seed viability 154 days after harvesting seedlings from the growth chambers using a 1% solution of 2,3,5-triphenyl tetrazolium chloride (TTC) seeds from the same collection as were used in the growth chambers, but which had not been planted.

Data Analysis. The software package R version 2.13.0 (R Core Development Team 2011) was used to run all statistical analyses. All tests were analyzed for differences between elevation categories rather than individual sites for the reasons stated above. Tukey Honest Significant Difference (HSD) tests were performed to test for differences in individuals between each of the three elevation categories. To illustrate the strength of highly significant differences found using the Tukey HSD test, post-hoc pairwise t-tests were performed using the conservative Bonferroni correction for p-values. The Bonferroni correction was not used in cases when differences were shown to be insignificant by a Tukey HSD test.

To analyze floral morphology traits, certain measurements were combined in order to create more meaningful variables for analysis: lip area was defined as lip width multiplied by lip length, and corolla volume was defined by the formula for an ellipsoid sphere:

$$(4/3)(\prod)(1/2(\text{corolla tube length}))(1/2((\text{corolla } 1 + \text{corolla } 2)/2))(1/2(\text{anthers to floor}))$$

The values that were obtained through these calculations were tested using a one-way ANOVA. Stem heights and fruit weights were analyzed the same way. Fruit:flower ratios were also analyzed by using one-way ANOVAs for percentage of fruits present on stems at each site. To analyze stem count per individual, a Chi-square test was used first to check for overall differences between individuals, then used a negative binomial generalized linear model and ANOVA with Chi-square test.

Differences in data obtained from the growth chamber experiment (time to germination, time to first true leaf, and overall growth rate) were tested by elevation category using linear models with one-way ANOVAs for model simplification. Overall growth rate was calculated by difference in height between the first and last measurements taken for an individual and divided by the number of growing days. Above- and below-ground biomass, days to germination and growth rates of seedlings from the growth chamber experiment were analyzed using one-way ANOVAs. Bootstrap analyses were used to test the relationship between above- and below-ground biomass to account for the small sample size ($N_{germinants} = 17$). Post-hoc tests were not run for any variables from the growth chamber experiment because of the small sample size.

Insect community composition data were analyzed to test for differences between sites using PERMANOVA analyses on all species observed and collected. The Shannon-Wiener index was calculated as a measure of insect species diversity at each elevation category. Proportion tests were performed on the 14 most common species found both in collections and observed visiting flowers, so as only to include the most likely pollinators. For this analysis, insects were broken down into small (<9mm long), medium (9-13mm long) and large (>13mm long) body size categories to test for differences in proportion of each insect size along the elevation gradient. Associated plant species were analyzed for community differences between sites using a PERMANOVA with binomial distribution because the data reflected only presence or absence of plant species at each site.

Results

Phenotype. Corolla tube volume differed significantly between elevations (F=5.05, d.f.=2, p=0.007, Fig. 3). Volumes at low elevation sites were significantly smaller than those at medium (p<0.009) and high elevation (p=0.03) sites, though there was no difference between medium and high elevation sites. When the traits used to obtain corolla volume were analyzed separately (Fig. 4), flowers at high sites were found to be not only larger in volume but differently shaped. The distance between the anthers and the corolla floor varied between elevation categories (F=4.76, d.f.=2, p=0.009) and was significantly greater in individuals at high elevation than low (p=0.01, Tukey HSD) and medium (p=0.04, Tukey HSD) elevation sites. Corolla tube length did not differ between low and high elevation sites but were significantly longer at medium sites than low (p<0.001) and high (p=0.01) elevation sites. Average corolla width and corolla width 1 did not differ among populations according to a one-way ANOVA. Corolla width 2 measurements were larger at high than low elevation sites (F=5.08, d.f.=2, p=0.006), and mouth diameters were significantly smaller at high than medium elevation sites (F=5.58, d.f.=2, p=0.004).

Upper and lower lip areas (Fig. 5) both varied significantly by elevation category (lower lip area: F=12.86, d.f.=2, p<0.001; upper lip: F=7.29, d.f.=2, P<0.001). Though lip areas did not differ between medium and low sites, individuals at high sites had significantly smaller lip areas (p<0.001). Average anther insertion and anther insertion 1 did not differ significantly between elevations, however, anther insertion 2 did (F=4.70, d.f.=2, p=0.009), with anthers at high sites being significantly more shallowly inserted than both medium (p=0.01) and low elevation sites (p=0.04). Staminode length was significantly shorter at high than low (p=0.01) or medium elevation sites (p<0.001).

Among sites, there was a significant difference in stem height (F=76.85, d.f.=2, p<0.001) and stem number (p<0.001). Stem height decreased with elevation (Fig. 6), with heights decreasing significantly at each elevation category (high to medium p=0.01, medium to low p<0.001, high to low p<0.001). Stem number per plant (Fig. 7) was significantly greater at medium elevation sites (F=22.35, d.f.=2, p<0.001) than at low and high elevation sites.

Fruit:flower ratios did not differ between low and high elevation sites, but were significantly lower at medium elevation sites (F=22.35, d.f.=2, p<0.001). Fruits collected from low elevation sites weighed significantly more (Fig. 8) than fruits from medium or high elevation sites (n=739, F=13.51, d.f.=2, p<0.001).

Associated plant and pollinator community. Pollinator community composition (Table 2) was significantly different among elevation categories (F=0, d.f.=2, p<0.001). The Shannon-Wiener diversity index was highest at low elevation sites and deceased up the elevation gradient, from 2.7 at low sites to 2.4 at medium sites and 1.8 at high sites. Proportion tests showed a significantly greater number of large insects at lower elevations (p<0.001, Figs. 9a and 9b). No difference was found in associated plant species (Table 3) among sites (F=0.86, d.f.=2, P=0.51).

Growth Chamber Experiment. Only 17 of 8400 seeds germinated throughout the duration of the experiment. Days to germination, days to first true leaf, and growth rate differed significantly between treatments (F=40.0, 29.7, and 122.82 respectively, d.f.=1 and $p<0.001$ for all variables). Days to first true leaf after germination differed significantly between sites and treatments ($p<0.001$) but not elevations ($p=0.77$). Mean root biomass (0.008 ± 0.001, 95%CI, n=204) significantly varied with the mean of shoot biomass (.0174 ± 0.019, 95%CI, n=204) according to a bootstrap test ($p<0.001$, 1000000 resamples). Shoot and root biomasses also differed significantly in each treatment (F=41.99 and 11.29 respectively, and d.f.=1, $p<0.001$ for both). Of the seeds where viability could be determined with reasonable accuracy using TTC viability assays, significant differences were found between elevations (F=11.01, d.f.=2, $p<0.001$). Medium elevation sites had the highest viability (Fig. 10), followed by low ($p=.28$), then high ($p<0.001$).

Seedlings took fewer days to germinate, grew faster, and produced more above- and below-ground biomasses in the elevated temperature condition, and the same results were found for seedlings from seeds collected at low elevations ($p<0.001$ in all cases, Table 4). While seedlings from low-elevation collections produced true leaves sooner from low elevations, they also produced true leaves sooner in the control (current temperature) treatment ($p<0.001$ for both, Table 4).

Discussion

As hypothesized, individuals of *P. palmeri* produced taller stems and more stems per plant, and larger fruits at lower elevations. Since elevation is frequently used as a proxy for elevated temperatures and climate change (Lookingbill and Urban 2005, Rodeghiero and Cescatti 2005, Gilbert 2010), these results may suggest that *P. palmeri* may become more robust as temperature increases in the future. Pollinator community composition differed significantly along the elevation gradient, supporting the second hypothesis, and low elevation sites contained the greatest Shannon-Wiener diversity index of insects. In plants such as *P. palmeri* which require an insect to at least partially enter the corolla tube to acquire nectar and pollen, larger pollinators could be expected to coexist with plants with larger flowers to fit their body sizes.

Phenotype. Flowers were smaller at lower elevations but differently shaped at each elevation category and insects were larger at lower elevations, indicating a more complex relationship between flower size and pollinators that can be explained by size alone. The lower lip of flowers of *P. palmeri* and other members of the Plantaginaceae family, serves as both a landing platform for visitors and a canvas for nectar guides (Free 1970), which helps usher visitors into the corolla vestibule. The smaller lips seen at higher elevations could be indicative of selective pressures placed on the plants by the behaviors or smaller size of pollinators at high elevations. The bearded staminodes found on *P. palmeri* increase effectiveness of pollen transfer from anthers to pollinators by acting as a lever that increases contact with the stigma, especially for bees (Walker-Larsen and Harder 2001). Like the other differences observed in floral characteristics, the shorter staminodes found at high elevations could be a result of selective pressures from a different and less diverse pollinator community than at lower elevations.

Another potential explanation for the inverse relationship between corolla size and pollinator size could be that lower pollinator diversity at high elevation sites and a possibly lower density of flowers (which was not measured in this study) is linked to the production of larger flowers that would increase overall floral display for more effective attraction of pollinators, making the display potentially more attractive to pollinators (Makino *et al.* 2007, Makino and Sakai 2007). Recent studies support this possibility by showing that pollinator community diversity varies with floral morphological traits (Ortigosa and Gómez 2009, Bluthgen and Klein 2011). Even given larger flowers at high elevations, greater pollinator community diversity can contribute to greater predictors reproductive success including higher fruit set and lower pollen limitation (Galloni *et al.* 2008, Gomez *et al.* 2010, Vergara and Badano 2009), though effects of pollinator community diversity on fruit weight and seed viability are understudied. If lower elevation sites represent conditions of warming produced by climate change, a greater diversity in the pollinator community associated with *P. palmeri* could indicate greater reproductive success for the species in the future.

The decrease in stem height up the elevation gradient may indicate fewer resources going towards production of vegetative material due to colder temperatures found at high elevations. Data from weather stations at La Verkin, UT (981.5m), Zion National Park, UT (1234.4m), and Lava Point, UT (2406.1m) show decreased mean temperatures in June and July at high elevations (Fig. 11). Sites used in this study fell into the elevation range (1352-1762m) between the Zion National Park and Lava Point weather stations, between which there was the largest difference in temperatures in June and July. Plant species in other systems have responded to increasing temperature gradients with earlier phenological development and faster growth rates (Xiao *et al.* 2001, Hollister *et al.* 2005, Sherry *et al.* 2008, Li *et al.* 2011). Collection of wind speed data would be necessary to determine whether or not there is a connection between wind speed experienced at medium elevation sites and vegetative productiveness, in addition to other variables such as the possibly shallower, more nutrient-poor soils at medium and high elevation sites due to proximity to the road. However, the fact that stem count was significantly greater at middle and high elevations suggests that plants at higher elevations may be producing the same amount of above-ground biomass, but with different growth patterns (a greater number of shorter stems), though data on above- and belowground biomass would be necessary to definitively find whether this is the case. Stem heights in other plant species have been shown to grow taller at lower elevations and higher temperatures (Klinka *et al.* 1996, Cuevas 2003), and if this trend holds in *P. palmeri* as it appears to do, the species may grow taller in response to climate change in the future. Another explanation for greater stem heights at lower elevations could be increased nutrient uptake at lower sites due to a prescribed fire in 2009 (Cheryl Decker 2010, pers. comm.), as soil nitrogen availability can increase after light to moderate fires (Vlamis and Gowans 1961, Kutiel and Inbar 1993).

Fruits collected from low sites, as hypothesized, weighed more than fruits collected from high sites. Possible explanations include higher temperature at low elevations, greater soil depth due to their location farther from the road bed. If higher temperature is the factor that has the greatest effect on fruit weight, prospects for using *P. palmeri* successfully in restorations in the future could be positive since greater fruit weight could indicate more seeds within a capsule or fewer but better provisioned seeds per capsule. One possible explanation for lower fruit:flower ratios at medium elevation sites is that these sites tended to be very windy (anecdotally, as wind velocity was not quantified in this study). Pollinator observations frequently showed insect visitors attempting but failing to land on a flower, occasionally for several minutes, before being blown away by the wind at medium elevation sites, which may have decreased frequency or effectiveness of pollination, and therefore explain the reduced fruit set at these sites. An expanded elevation range could clarify whether low fruit-to-flower ratios at medium elevation sites could have been due to temperature, making the trait susceptible to climate change.

Differences in phenotype could be due to genetic or environmental factors including temperature (Murcia 1990, Higuchi and Utsunomiya 1999) or edaphic conditions (Mal *et al*. 1997) that were not accounted for in this study. Future research on the effects of climate change on phenotype of *P. palmeri* and other species used in restorations should include a more comprehensive survey of surrounding vegetation and soil characteristics and temperatures to assess whether vegetative and floral traits might be linked to these variables. Further germination and viability analyses would clarify the relationship between fruit weight and seed set and viability in *P. palmeri*.

Growth Chamber Experiment. Although growth rate, days to germination and days to first true leaf differed by treatment and elevation, germination rates were extremely low (0.002%). However, data acquired from the experiment are suggestive of trends in which *P. palmeri* seedlings may develop more rapidly at higher temperatures and elevations. These findings, if they hold true at a larger scale, could have important implications for restorations. If seed is being sown in a disturbed area to anchor soil and prevent nutrient leaching, for example, the development rate of resulting seedlings could impact how well the plants fit the needs of the management plan.

Root biomass increased at a slower rate than shoot biomass leading to root:shoot ratios less than one in all seedlings, contrary to what would be expected from the limited work that has been done on mature arid-environment plants, which generally develop root:shoot ratios greater than one according to meta-analyses of plants across functional groups (Mokany *et al*. 2005).

Because not much work has been done on root-shoot biomass relationships in arid environments (Mokany *et al*. 2005), seedling root:shoot biomass ratio may not be indicative of mature plant root:shoot ratio.

During the experiment, a film of fungi and algae developed on top of the soil, which could have inhibited germination, as could possible bacterial infection. The low germination rate could be due to low seed viability, as revealed by post-experiment tetrazolium chloride assays. Previous germination trials indicate that *P. palmeri* seeds generally do not require cold stratification or scarification to produce high germination rates, though some populations benefit from treatment (Meyer and Kitchen 1992, Meyer and Kitchen 1994, Meyer *et al.* 1995). It is possible that seeds from the populations sampled for this study require or would benefit from pre-treatment. Performing a similar growth chamber experiment after a germination trial and applying fungicide or algicide to prevent their growth on cells might also yield higher germination rates.

Another step that could be taken in this study would be to test for genetic differences in populations using molecular techniques and common garden studies to further understanding of whether differences observed in the field were due to phenotypic plasticity or genetic variation. Future research should test for difference in growth patterns in ambient and elevated CO_2 conditions to see what effects the predicted increases in CO_2 will have on the growth and phenotype of *P. palmeri*, since this is an important factor in conjunction with temperature in the behavior of a species in the future climate (Coleman and Bazzaz 1992, Ahmed *et al*. 1993, Stirling *et al*. 1998, Williams *et al.* 2000). Since the climate in the Colorado Plateau is also predicted to become more arid, with less rainfall and more evaporation (IPCC 2007), experimental water limitation manipulations would also be an interesting avenue for future research. Expanding this study to other species useful in restoration is important to attain a suite of species for which scientists and managers are informed about their behaviors and responses to environmental changes.

A wide range of confounding biotic and abiotic factors makes predicting responses of plant species and populations to climate change difficult (Melles *et al*., 2011). The conclusions of this study would be strengthened by a greater diversity of types of data including more detailed information on plant and insect community composition, soil qualities and recent disturbances. It would also be interesting to expand the elevation range of sites to test whether patterns found in this study intensify at range boundaries, as climate is expected to influence phenological dynamics more at range boundaries than in range interiors (Parmesan and Yohe, 2003).

Conclusions. This study is a first step in understanding how *P. palmeri* might respond to climate change over its entire range and is meant only to illustrate how the species might behave in response to climate change at a local level. My results suggest phenotypic changes but no apparently adverse effects of *P. palmeri* in response to elevation or warming (as exhibited in both the growth chambers and the elevational temperature differences) on productive capacity, meaning it is likely to remain a strong candidate for use in restorations and reseedings at least 50 years into the future. Pollinator community composition and diversity may be affected by temperature or by shifts in floral morphology and should be monitored to better understand the driving factors influencing plant reproductive ability in response to climate change. This study adds to the knowledge base of the plant species and plant-pollinator relationships in the semi-arid southwestern U.S. and highlights the value of similar research given the typically slow recovery time of these species post-disturbance and the increasing need for restoration and post-fire reseeding.

Accumulating knowledge on the vegetative and reproductive response of plant species used in restorations to climate change will allow management agencies to determine where and when it would be most appropriate to use these species in restorations, as well as informing them of how they might be expected to fare in the future in their native habitats. Since *Penstemon* is widespread genera throughout the western United States, the findings from this study can be used as a springboard for other similar studies and be useful to the conservation and management of these species both within and outside of Zion National Park. The variability of ecosystem types on the Colorado Plateau and the inclusion many national and state parks make conservation of this area's ecosystems valuable not only ecologically, but socially and financially.

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Tables

Table 1. Site numbers, locations, and grouped elevation categories used in analyses. Italicized numbers indicate elevation differences between categories.

Site Number	GPS Coordinates (NAD 27)	Elevation (m)	Elevation category	Elevation difference to next highest site (m)	Average difference within elevation categories (m) +/-1 s.d.
1	37.266967 N 113.108858 W	1352	Low	18	23.0+/-8.7
2	37.269272 N 113.106117 W	1370	Low	18	--
3	37.270764 N 113.103078 W	1388	Low	33	--
4	37.272589 N 113.100356 W	1421	Low	*51*	--
5	37.279214 N 113.101258 W	1472	Medium	15	17.0+/-2.8
6	37.280339 N 113.100744 W	1487	Medium	19	--
7	37.280706 N 113.098619 W	1506	Medium	*81*	--
8	37.292547 N 113.095828 W	1587	High	73	58.3+/-37.2
9	37.298075 N 113.100206 W	1660	High	86	--
10	37.302258 N 113.102511 W	1746	High	16	--
11	37.304533 N 113.101267 W	1762	High	--	--

Table 2. Mean measurements of floral characteristics (n=273) at each elevation category. P-values indicate overall differences between elevation categories.

Measurements	Low	Medium	High	P-value
Corolla length (mm)	15.7	16.9	16.1	<0.001
Staminode length (mm)	22.2	23.4	20.5	<0.001
Anthers to floor (mm)	12.1	12.2	12.8	0.009
Mouth diameter (mm)	13.4	13.6	13.9	0.004
Corolla 1 (mm)	12.5	12.7	12.8	0.36
Corolla 2 (mm)	13.3	13.7	13.8	0.007
Corolla volume (mm^3)	1301.3	1447.8	1426.1	0.002
Upper lip width (mm)	15.9	16.3	15.9	<0.001
Upper lip length (mm)	4.3	4.6	4.1	0.005
Upper lip area (mm^2)	69.4	74.9	64.1	<0.001
Lower lip width (mm)	17.6	17.6	15.1	<0.001
Lower lip length (mm)	10.1	10.4	9.5	0.01
Lower lip area (mm^2)	179.4	183.4	151.3	<0.001

Table 3. Insects collected and observed, identified to the lowest taxonomic level possible, present at each elevation category. An asterisk (*) next to a name indicates an insect type used in proportion tests to test for differences in percentages of pollinator community size classes among sites.

Species	Low	Medium	High
Agapostemon spp.*	X	X	X
Ammophila procera*	X	X	
Anthidium illustre*	X	X	
Apidae 1*		X	
Apidae 2*	X		
Apidae 3*	X	X	X
Apidae 4*	X	X	X
Bombus ternarius*	X		
Bradonidae spp.	X		
Ceratina spp.*	X	X	X
Cicadellidae 1	X	X	
Cicadellidae 2	X		
Coleoptera 1*	X	X	X
Coleoptera 2	X	X	X
Coleoptera 3	X		
Coleoptera 4	X		
Coleoptera 5	X	X	
Coleoptera 6		X	X
Coleoptera 7	X		
Diadasia spp.*	X	X	
Diptera 1			X
Diptera 2			X
Diptera 3	X		
Diptera 4	X	X	
Diptera 5		X	
Diptera 6		X	
Diptera 7		X	
Dorymyrmex bicolor	X	X	X
Euphilotes spp.*	X	X	
Formicidae 1	X	X	X
Formicidae 2	X		
Formicidae 3	X	X	
Formicidae 4	X		
Formicidae 5		X	
Formicidae 6	X	X	
Hymenoptera 1	X		
Hymenoptera 2	X	X	
Formicidae 7	X	X	
Osmia spp.*	X		
Perdita spp.*	X	X	

Table 4. Associated species, identified to the lowest taxonomic level possible, present at each elevation category within a 25m radius of focal plants.

Species	Low	Medium	High
Arctostaphylos patula			X
Asclepias spp.		X	
Asteraceae spp.	X		
Astragalus spp.	X	X	
Bromus tectorum	X	X	
Cryptantha spp.	X		
Datura stramonium	X		
Ephedra viridis		X	
Erigeron spp.	X		
Euphorbia albomarginata	X	X	
Geranium spp.		X	
Helianthus spp.	X		
Juniperus osteosperma		X	X
Lotus utahensis	X		
Lupinus argentus	X		
Opuntia spp.	X	X	X
Papaveraceae spp.	X		
Penstemon palmeri	X	X	X
Poaceae spp.	X	X	
Polygonum douglasii	X		
Quercus turbinella			X
Senecio vulgaris	X	X	
Sphaeralcea parvifolia	X		
Swertia albomarginata		X	

Table 5. Mean values for each measurement collected from seedlings in growth chambers. Values in the Control column come from growth chamber set to current temperatures, treatment values come from growth chamber set to projected future temperatures. Values in low, medium, and high columns are measurements from seeds collected at each elevation category. All values are significantly different between control and treatment, and between low and high.

Measurements	Control	Treatment	Low	Medium	High
Days to germination (days)	38.86 ± 1.54	26.35 ± 3.45	34.01 ± 1.57	--	48.00 ± 2.54
Growth rate (mm/day)	0.20 ± 0.01	0.37 ± 0.03	0.24 ± 0.02	--	0.18 ± 0.01
Days to first true leaf (days)	7.19 ± 0.68	11.61 ± 0.18	7.83 ± 0.69	--	8.20 ± 1.69
Root biomass (g)	0.007 ± 0.001	0.012 ± 0.004	0.009 ± 0.001	--	0.008 ± 0.001
Shoot biomass (g)	0.014 ± 0.001	0.031 ± 0.009	0.018 ± 0.002	--	0.013 ± 0.002

Figures

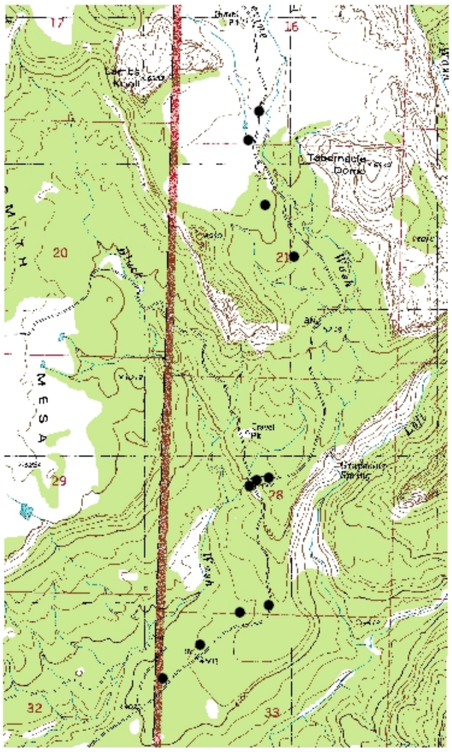


Figure 1. Topographical map of study sites, all of which were located within Zion National Park. Western Park boundary is marked by a red line and sites are marked with black circles. GPS coordinates can be found in Table 1.

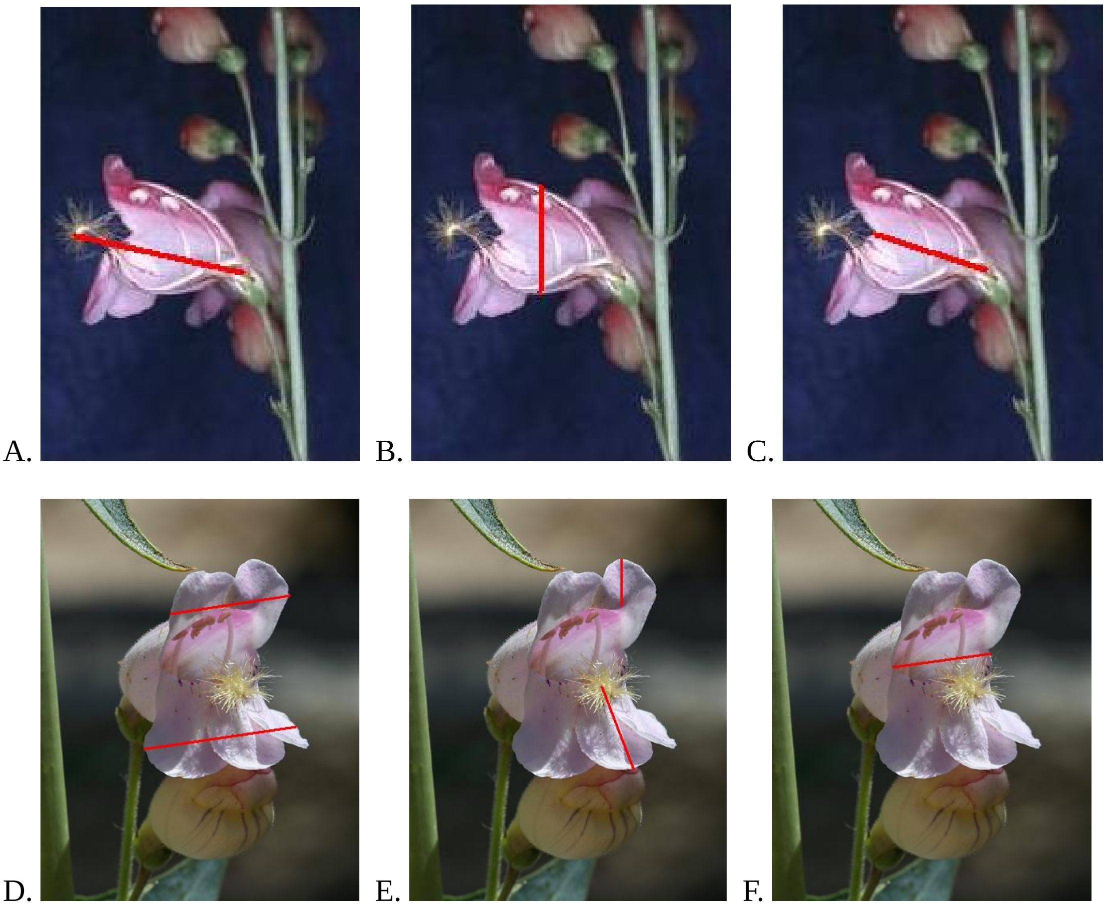


Figure 2. Floral measurements. A.) staminode length, B) anthers to floor, C) corolla length, D) upper and lower lip widths, E.) upper and lower lip lengths, F.) mouth diameter. Two more measurements of corolla width (corolla diameters 1 and 2) were taken on the same axis as mouth diameter, at 2/3 increments down the corolla tube.

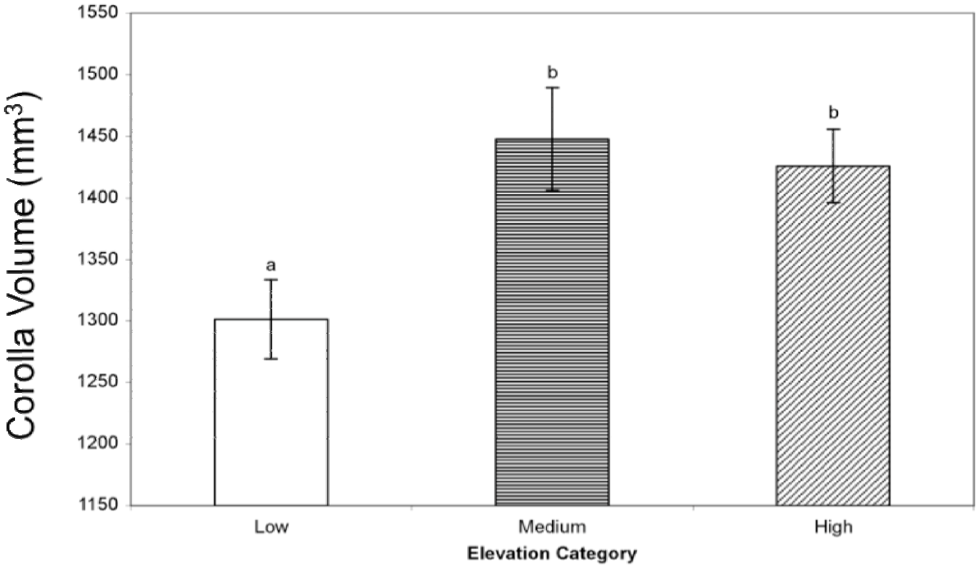


Fig. 3. Mean corolla volume (n=273, ± S.E.) at each grouped elevation category. Bars with different letters are significantly different at P ≤0.05 based on Tukey HSD tests comparing traits across elevations.

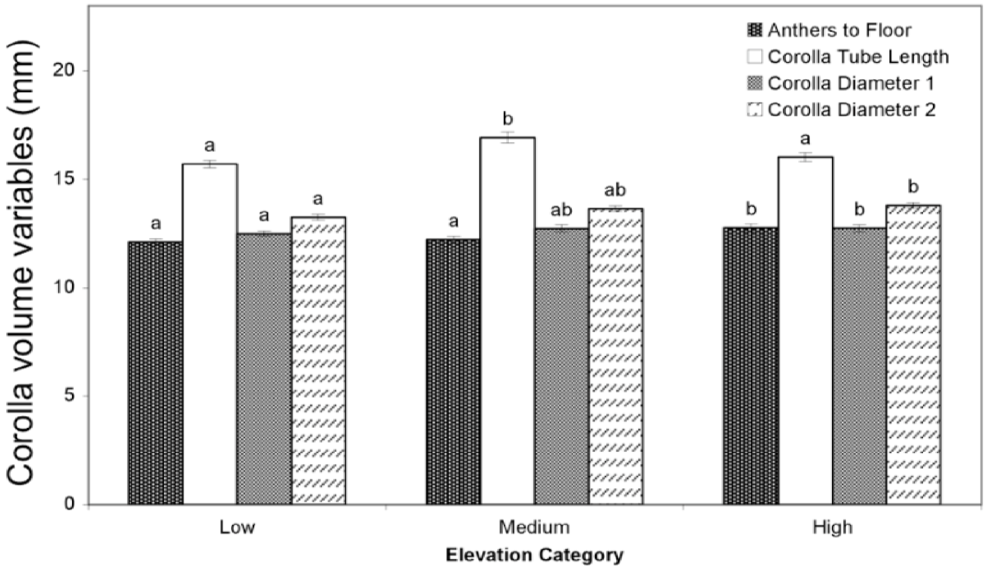


Fig. 4. Mean length of floral variables used in the calculation of corolla volume (n=273, ± S.E.) at each grouped elevation category. Bars with different letters are significantly different at P ≤0.05 based on Tukey HSD tests comparing traits across elevations.

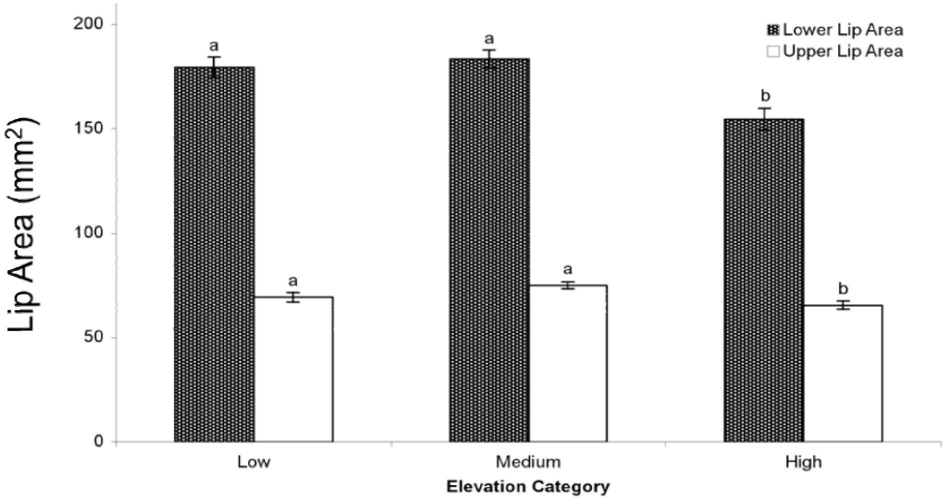


Fig. 5. Mean lip area (n=273, ±S.E.) at each grouped elevation category. Bars with different letters are significantly different at P ≤0.05 based on Tukey HSD tests comparing traits across elevations.

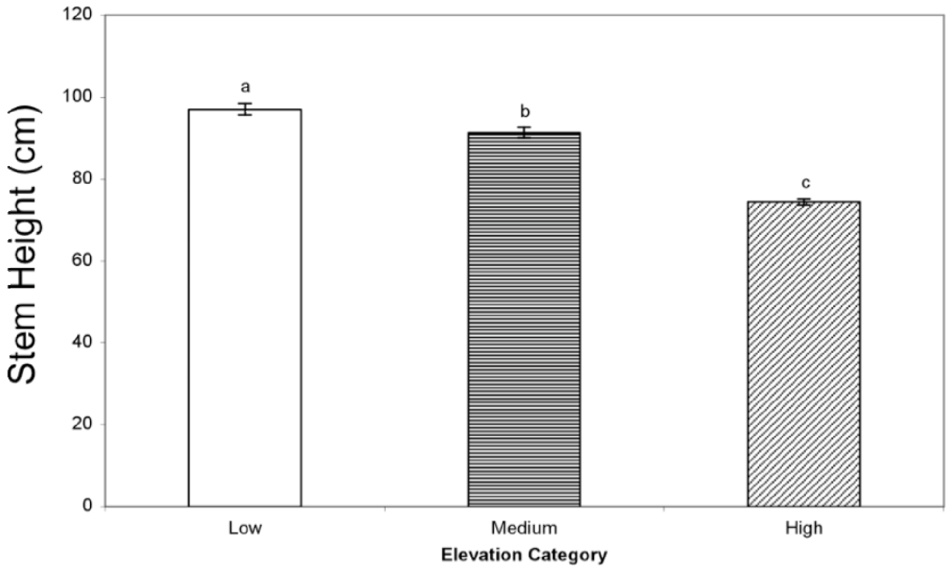


Fig. 6. Mean stem height (n=1790, ±S.E.) at each grouped elevation category. Bars with different letters are significantly different at P ≤0.05 based on Tukey HSD tests comparing traits across elevations.

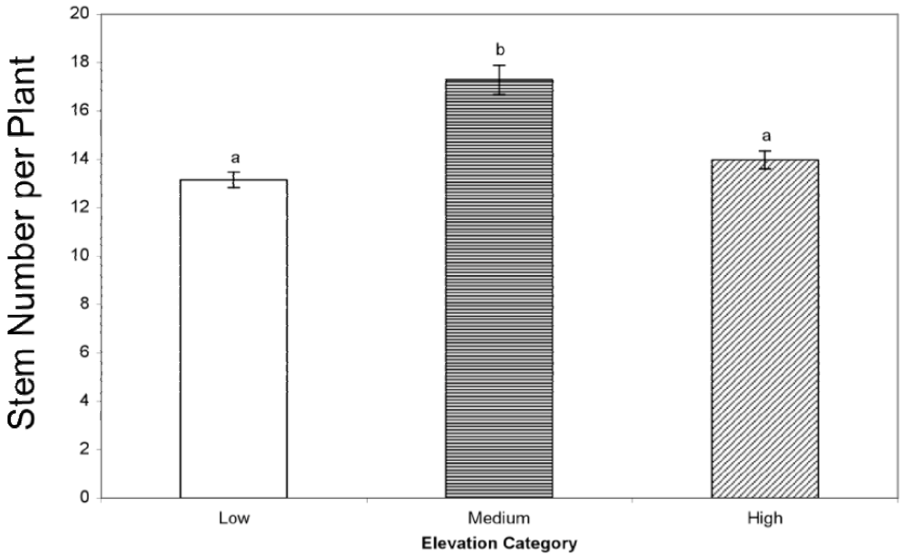


Fig. 7. Mean number of stems per plant (n=1790, ±S.E.) at each grouped elevation category. Bars with different letters are significantly different at P ≤0.05 based on Tukey HSD tests comparing traits across elevations.

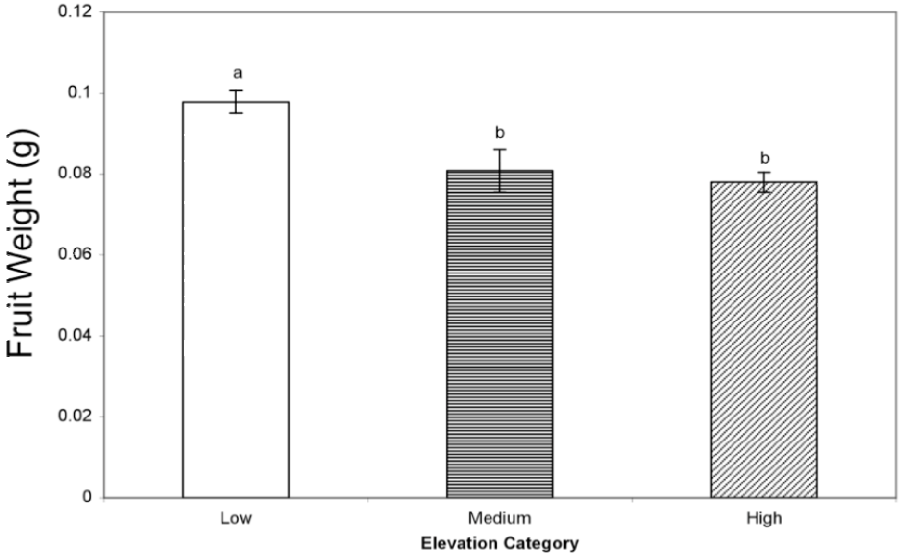
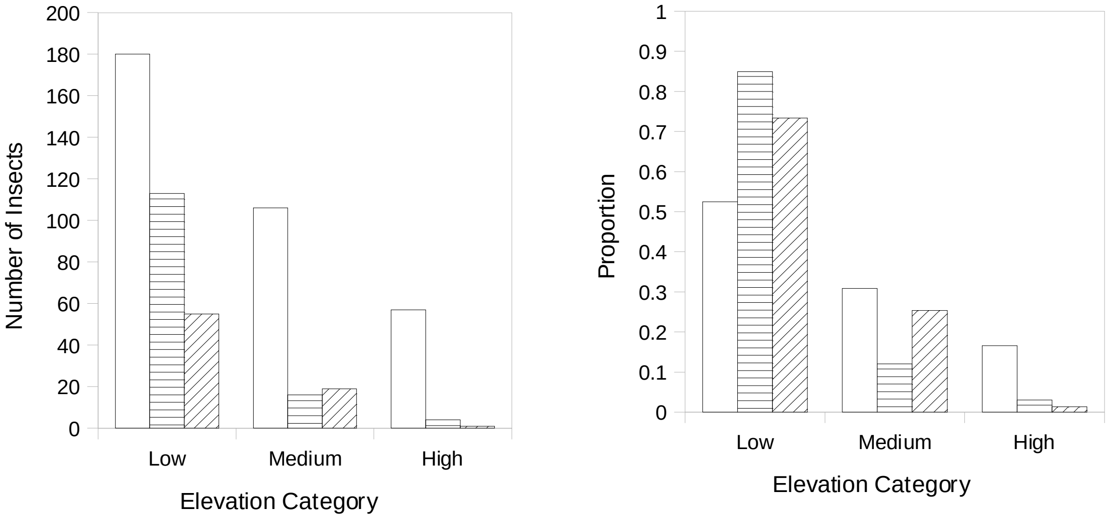


Fig. 8. Mean fruit weight (n=754, ±S.E.) at each grouped elevation category. Bars with different letters are significantly different at P ≤0.05 based on Tukey HSD tests comparing traits across elevations.



A. B.

Fig. 9. In each elevation category and from left to right, bars represent values for small insects (<9mm), medium insects (9<<13mm), and large insects (>13mm). A) Number of insects of each body size class found at each elevation category. B) shows the proportions of each insect size class present at each elevation category.

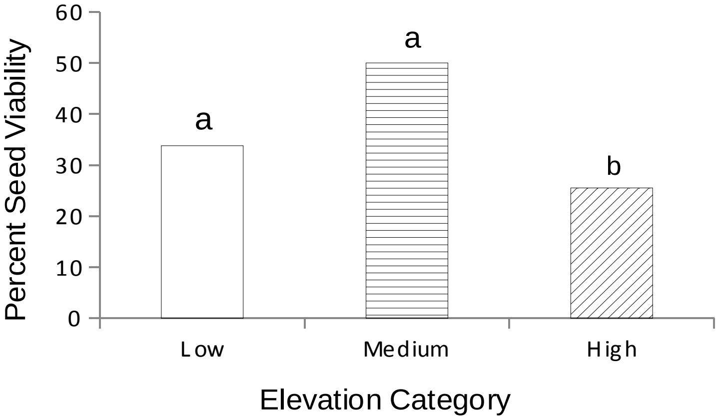


Fig. 10. Viability of seeds collected (n=403, ±S.E.) from each elevation category. Bars with different letters are significantly different at P ≤0.05 based on Tukey HSD tests comparing viability across elevations.

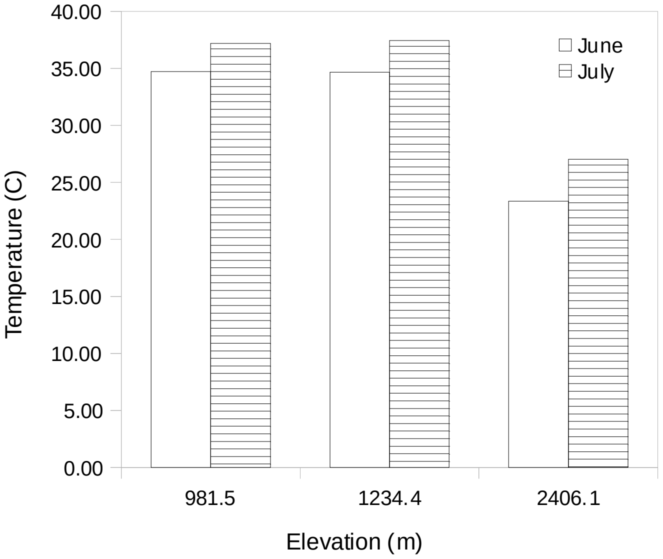


Fig. 11. Mean temperatures at weather stations at three elevations in and around Zion National Park during June and July.