Estimating how climate affects sexual and asexual reproduction in Desert yellowhead (*Yermo xanthocephalus*)

Joy Handley and Lusha Tronstad

Wyoming Natural Diversity Database, University of Wyoming, Laramie, Wyoming

Suggested citation: Handley, J., and L.M. Tronstad. 2022. Estimating how climate affects asexual and sexual reproduction in Desert yellowhead (*Yermo xanthocephalus*). Report prepared by the Wyoming Natural Diversity Database, University of Wyoming for the Wyoming Bureau of Land Management.

ABSTRACT

As air temperatures rise, the rates of sexual and asexual reproduction may change in plants. Plants may put more resources toward sexual reproduction in favorable conditions and switch to asexual reproduction when conditions become more stressful. Plant species that are capable of asexual and sexual reproduction must partition energy between these strategies which involves compromises. We measured how climate altered the sexual and asexual reproduction of Desert yellowhead (*Yermo xanthocephalus*), a rare member of the Asteraceae known from two populations in Wyoming. We measured precipitation, air temperature and soil moisture while also measuring seed (sexual reproduction) and ramet (asexual reproduction) production over a two-year period. Overall, Desert yellowhead produced few viable seeds; 15% of seeds were viable from pollinated flowers at the Sand Draw populations and only 1% were viable from the Cedar Rim population. Conversely, Cedar Rim produced twice as many ramets compared to Sand Draw. Sand Draw likely has more suitable conditions for Desert yellowhead, such as more stable soil moisture and more protection, which resulted in higher rates of sexual reproduction. Cedar Rim appeared to have less suitable conditions, such as more variable soil moisture and more exposure, resulting in higher asexual reproduction. Comparing sexual and asexual reproduction in rare and endemic plants can supply information about how populations are functioning, and provide insight about their potential persistence and resilience to future perturbations.

INTRODUCTION

Climate models predict higher air temperatures, and more evapotranspiration in Wyoming throughout the century (Sharma et al. 2020) which may reduce the survival of individual plants (Vincent et al. 2020). As summer temperatures rise, plant reproductive processes may be altered (Hacket-Pain and Bogdziewicz 2021, Pau et al. 2018) including sexual (i.e., seed production through transfer of pollen among plants) and asexual methods (e.g., vegetative growth of ramets from rhizomes, stolons or similar structures; Straka and Starzomski 2015; Pearse et al. 2017; Wang et al. 2018). Heat stress in plants can decrease sexual reproduction by reducing pollen viability and ovule development (Sita et al. 2017). Drier conditions can reduce sexual reproduction, as observed in the rare Chrysanthemum tree (*Nouelia insignis*) in south-central China (Liu et al. 2021). Drought can also change the ratio of sexual to asexual reproduction by increasing the cost of sexual reproduction and slightly decreasing the cost of asexual reproduction (Wang et al. 2018). These changes were due to lower seed-set and a sharp decline in the survival rate of saplings, while ramets were produced closer to the mother plant so there were fewer resources invested in the Narrowleaf peashrub (*Caragana stenophylla*) in northern China. Understanding how a changing climate may effect plant reproduction is critical to make informed decisions to maintain population viability and genetic diversity.

The method of reproduction can have repercussions for the persistence and viability of plant populations. Sexual reproduction increases the genetic diversity within populations making them more likely to survive less favorable conditions (Jabis et al. 2011). For example, the rare Yellow horned poppy (*Glaucium flavum*) relies on a seedbank to endure at the northern edge of its distribution in Norway (Solås et al. 2007). Conversely, asexual reproduction produces new plants that are genetically identical to the parent plant creating populations that are less resilient (Agrawal 2001). The rare Sea holly (*Eryngium maritimum*) primarily propagates asexually through a root bank in Norway (Curle et al. 2007). Asexual reproduction provides a more secure method of maintaining a population in the short-term, while the genetic diversity provided through sexual reproduction is necessary for supporting the population long-term (Brzyski et al. 2014; Lin et al. 2016). Therefore, the Yellow horned poppy may persist longer under a changing climate because this plant maintains genetic diversity through seed production compared to Sea holly that mainly produces clones. Sexual reproduction has costs, since seeds require more energy to produce and seedlings have lower survival rates compared to ramets (Herben et al. 2012; Wang et al. 2018). Plant species that are capable of both methods may change the ratio of sexual to asexual reproduction depending on environmental factors (Eriksson and Bremer 1993; Lin et al. 2016; Wang et al. 2018). Measuring the ratio of sexual to asexual reproduction in plants can be critical to estimate the potential resilience of a species in the future, especially those with a limited distribution.

Rare and endemic plants are critical members of plant communities that often perform essential ecosystem functions (e.g., nutrient cycling), and can make communities more resistant to the invasion of exotic plants (Xu et al. 2020; Lyons and Schwartz 2001); however, little is known about the reproduction of many rare and endemic species (Lyons et al. 2005; Burmeier and Jensen 2008; Miller et al. 2019). Rare species often have low densities and endemic species have a limited geographic range (Lyons et al. 2005; Broennimann et al. 2005) which increases their probability of extinction (Flather and Sieg 2007). Knowledge of a plant’s reproduction is critical to understand a species’ current trend and their ability to persist (Curle et al. 2007; Solås et al. 2007; Crawford et al. 2022). Rare species, in particular, can be more sensitive to changes in temperature and precipitation (Vincent et al. 2020). Information about the ecology of rare and endemic species is essential for making informed management decisions (USDI 2001, 2010) for the persistence of their populations.

We measured how climate altered the sexual and asexual reproduction of Desert yellowhead (*Yermo xanthocephalus*), a rare and endemic plant listed Threatened under the US Endangered Species Act. Desert yellowhead, a member of the Asteraceae (Daisy family), is known from two populations in central Wyoming. Seed viability was extremely low in both populations in 2018 (15% and 0%), but the transfer of pollen by pollinators did not limit seed production (Handley and Tronstad 2021). We postulated that climate may alter sexual and asexual reproduction of Desert yellowhead. We measured seed and ramet production while measuring temperature, precipitation and soil moisture to estimate the degree to which Desert yellowhead uses these reproductive methods in each population. Our specific questions were: 1) How do precipitation, temperature and soil moisture differ between the populations? 2) To what extent does climate recorded within the populations differ from the closest weather stations? 3) To what extent did Desert yellowhead use sexual and asexual reproduction in each population? and 4) How do differences in climate and reproductive method differ between the populations? Results will provide information to managers about how climatic factors alter the reproduction of a rare and endemic plant, and the trade-offs between sexual and asexual reproduction.

METHODS

Study Species and Background Information

Desert yellowhead grows in sparsely vegetated sagebrush steppe and cushion plant communities (Fertig 1995, Scott and Scott 2009, Heidel et al. 2011) and the species is only known from a 10 km^2 area with distinctive conditions in central Wyoming. The unique pale beige soil resembles the volcanic sandstone and tuff parent material (Van Houten 1964; Scott and Scott 2009, Heidel et al. 2011) and may limit the plants that are able to grow there. This unique plant was discovered by Robert Dorn in 1990 at Sand Draw (Dorn 1991) and a second population, Cedar Rim, was found ~8 km downwind in 2010 (Heidel et al. 2011). Desert yellowhead (Figs. 1a, b) was listed as Threatened under the US Endangered Species Act in 2002 (USDI Fish and Wildlife Service 2002). Desert yellowhead occurs at ~2100 m elevation in a cold desert climate (Beck et al. 2018), which received an average of 25 cm of precipitation annually (Western Regional Climate Center 2022, Jeffrey City). The Sand Draw population is much larger (9,200-13,250 plants; Scott and Scott 2009; Doak et al. 2016; Dibner et al. 2019) than the Cedar Rim population (~750 plants; Freeland, personal communication). The Sand Draw population is in a small, shallow basin formed by snowmelt and wind erosion (Scott and Scott 2009; Fig 1c). A large butte abuts the population to the north along with a low rim along the western edge that protects the population to some degree. The Cedar Rim population grows along the slopes of a small escarpment. Small drainages allow limited snow accumulation, but the topography provides much less capacity for snow storage (Fig 1d).

Desert yellowhead reproduces sexually and asexually. The yellow flowers produced on stalks bloom in late June to early July annually. Each flowerhead had one to ten florets and each floret had the potential to produce one seed (Fig. 1b). Seeds are produced sexually and self-pollination occurred infrequently (Handley and Tronstad 2021). Desert yellowhead reproduces asexually through underground structures that develop into rosettes. We have not excavated roots to verify the type of growth because the plant is federally protected. We assume these structures are ramets after examining specimens in the Rocky Mountain Herbarium and observations from previous investigations (Scott and Scott 2009).

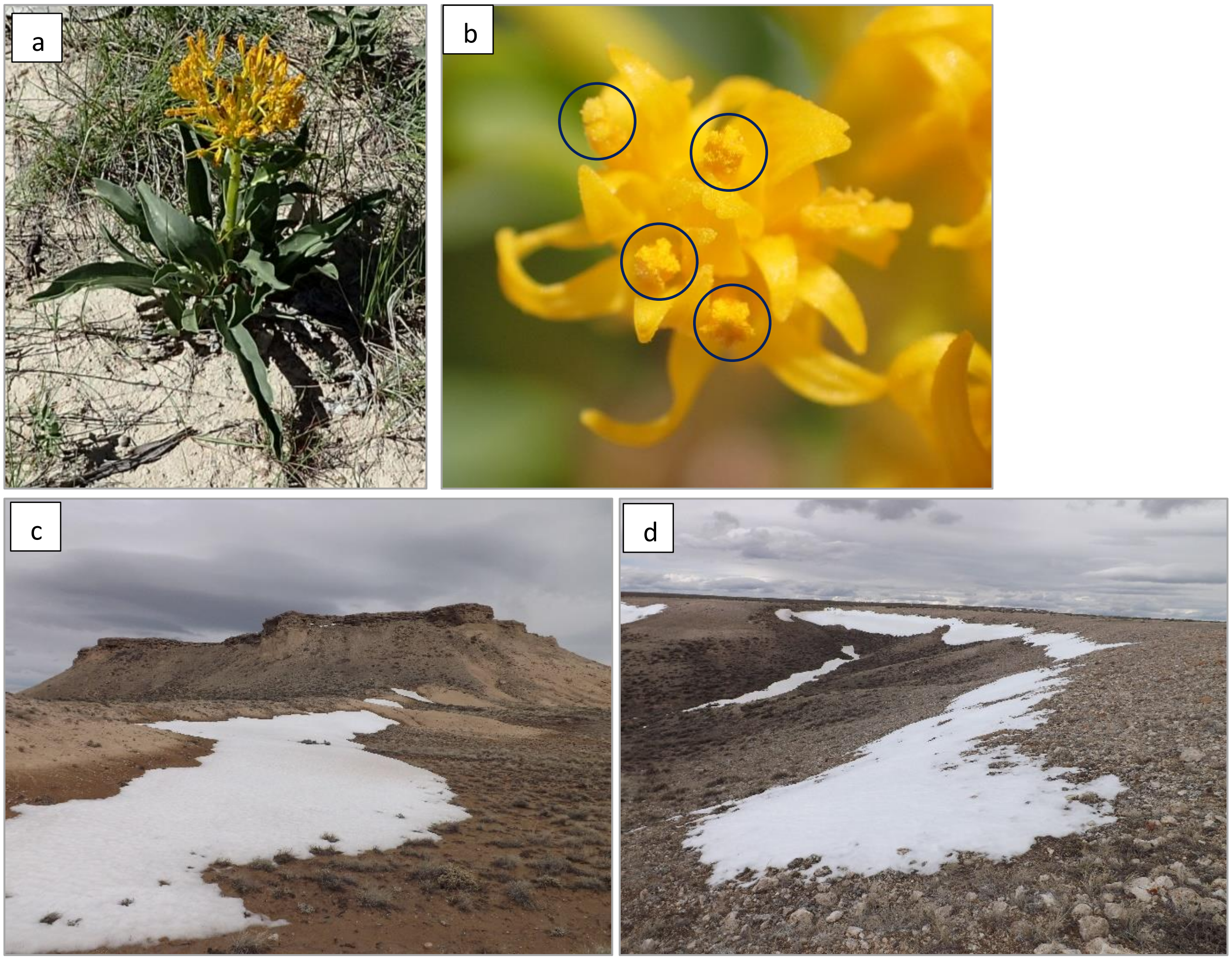


Figure 1. a) Desert yellowhead (*Yermo xanthocephalus*) plant in full bloom. b) A Desert yellowhead flowerhead showing four florets (circled). Accumulated snow during late spring at c) Sand Draw and d) Cedar Rim.

Climate measurements

We set up five weather stations (three at Sand Draw and two at Cedar Rim) to estimate how the climate differed between populations. Sensors measured precipitation, temperature and soil moisture from May to September (Fig. 2). Weather stations were enclosed with commercial woven wire fencing wrapped around three t-posts forming an equilateral triangle with ~2 m long sides and 1.4 m high. We used a 0.2 mm Rain Gauge (2m cable; Onset Computer) Smart Sensor to measure precipitation mounted 1.4 m high on a t-post. We deployed a HOBO Pendant® MX Temperature/Light Data Logger to measure temperature at the soil level, covered with a mound of rocks for shade. We measured soil moisture using two probes at two locations; one probe was adjacent to a Desert yellowhead plant and the other probe was at least 30 cm from Desert yellowhead plants. We deployed two lengths of soil moisture probes. Short probes (EC5 Soil Moisture Smart Sensor; Onset Computer) were 89 mm long and measured 0.3 L volume of soil. Long probes (10HS Soil Moisture Smart Sensor; Onset Computer) were 160 mm long and measured 1 L volume of soil. One weather station at each population had a pair of short probes. Two weather stations at Sand Draw and one weather station at Cedar Rim had a pair of long probes. The data loggers recorded from 28 April to 20 September 2021 and from 20 April to 11 October 2022.

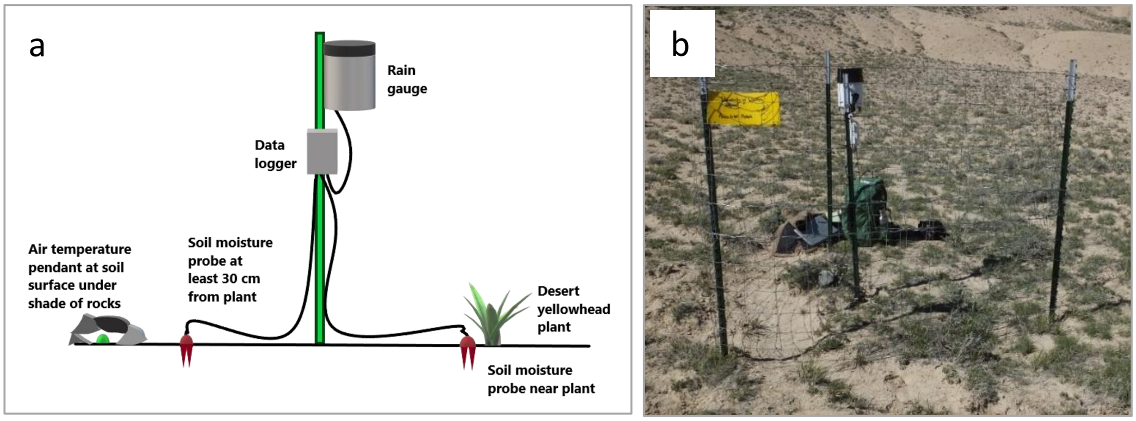


Figure 2. a) Schematic of a weather station with a rain gauge, air temperature sensor and two soil moisture probes. b) Photo of a weather station showing the enclosure with commercial woven wire fencing and the sensors in the middle.

Seed-set Experiments

We selected Desert yellowhead plants at the Cedar Rim population (18 plants in 2021 and 15 plants in 2022) and at the Sand Draw population (19 plants in 2021 and 16 plants in 2022) to estimate seed production. Before individuals bloomed (mid-June), we selected three flowerheads on each plant to receive one of each treatment. Bagged treatments restricted pollinator access and measured the degree to which flowers can self-pollinate. Open treatments left blooms available for local pollinators to visit and measured the number of seeds produced under ambient conditions. The hand-pollinated treatment added excess pollen in addition to pollen transported by pollinators to measure seed production when pollen was not limiting. Pollen for hand-pollination came from plants >50 m away and we delicately brushed collected anthers on the stigma of the treatment bloom. Some plants in each population got pollen from the other population, to compare outcrossing between the two populations and within populations. Blooms were bagged with 0.8mm mesh bags before (bagged treatment) or after (open and hand-pollinated treatments) flowers bloomed to contain the developing seeds. We monitored treatments through the summer and we collected seeds when flowerheads were ripe (mid-July to mid-August).

Flowerheads were placed in paper bags, returned to the laboratory and dried, then frozen for 15 days as a cold treatment.

We cleaned, counted, and weighed all the seeds to estimate the degree to which Desert yellowhead self-pollinated or depended on pollinators. We divided seeds that appeared non-viable and viable based on size and appearance. We counted the number and measured the mass of seeds that appear non-viable and viable separately for each flowerhead. We used Tetrazolium staining to test for viability which estimates the germinative potential of seeds by turning red to indicate cellular respiration (Lindenbein 1965). We compared the number of seeds that we visually assess as viable to the number of seeds that were viable according to Tetrazolium assays to evaluate our visual accuracy. We placed the seeds between moistened paper towels for 24 hours, cut them to expose the endosperm, and immersed them in tetrazolium solution for 24 hours. The endosperm of viable seeds turned pink or red and the endosperm of non-viable seeds remained white. We measured seed-set in 2018 (Handley and Tronstad 2021) and we included that data in our analysis.

Ramet monitoring

We measured ramet characteristics directly around individual plants to estimate asexual reproduction. We measured ramet characteristics on the same plants we selected for the seed-set study and additional plants with flowering stalks so that 80 plants were measured. We placed a 30 cm diameter hoop with the plant located in the middle to measure ramet characteristics for each individual. We assumed rosettes within the hoop (i.e., within 15 cm of the central flowering stalk and ≥2 cm space between ramets or ramet and parent plant; Fig. 3) were ramets from a Desert yellowhead plant. We chose a 15 cm radius based on a specimen of Desert yellowhead in the Rocky Mountain Herbarium (*Heidel 3441*). We assumed that seeds would germinate >15 cm from the parent plant, because seeds are dispersed by wind. We counted the number of ramets, the number of leaves per ramet, and we measured the longest leaf per ramet (proxy of ramet growth) in each hoop plot. The number of ramets and longest leaf length per ramet was measured at peak flowering (mid- to late June) and when the seeds were ripe (early to mid-August). We also counted the number of flowering stalks and flowerheads per flowering stalk in each hoop plot to estimate the number of seeds produced with the aim of evaluating asexual versus sexual reproduction. Individual Desert yellowhead plants do not produce flower stalks every year and some plants may produce more than one flower stalk in any given year.

Figure 3. Hoop plot with one flowering stalk. This flowering stalk had 40 flowerheads and one ramet (upper left in hoop). One flowerhead is bagged to exclude pollinators for the seed-set experiment.

Comparing sexual and asexual reproduction

We calculated the ratio of the number of viable seeds to the number of ramets for each plant we monitored. We measured the number of viable seeds from ~20 plants per population in the seed-set experiments. We estimated the total number of seeds produced per plant using the percent viable seeds in the open treatments and multiplied by the number of flowerheads for each plant. For plants not included in the seed-set experiment, we used the mean percent viable seeds in the open treatment by population and multiplied by the number of flowerheads. Asexual reproduction was estimated from the number of ramets produced. We calculated the ratio of sexual to asexual reproduction by dividing the number of viable seeds per plant by the number of ramets produced. We used this ratio to evaluate how each plant partitioned energy resources in each population between years.

Data analysis

We used generalized linear models (glm) to calculate differences in precipitation and mixed effects models (lmer) to estimate differences in air temperatures. We summarized climate data measured in 15-minute increments by site (Cedar Rim or Sand Draw), month (May to September), year (2021 or 2022), and probe type (short or long). We did not include the station identification as a random effect for precipitation because the effect was zero causing singularity. We calculated mean, maximum and minimum daily air temperatures by month, site and year with station identification as a random effect to include differences in microclimates. We used estimated marginal means (emmeans) to calculate p-values and differences within factors (Lenth 2021). We compared precipitation and air temperatures (mean, maximum and minimums calculated from daily values) between data gathered within the Desert yellowhead populations (Sand Draw and Cedar Rim) to the nearest weather stations at Jeffrey City (ca 45 km from the Desert yellowhead populations) and Riverton (ca 60 km from the Desert yellowhead populations), Wyoming (Western Regional Climate Center 2022) to see if the weather stations could be used to estimate climate at our study site. We did not perform statistical analysis on these data, because only monthly data were available from the weather station which was not enough to estimate differences.

We used mixed effects models (glmer) to investigate differences in the number of seeds, mean mass of seeds and the proportion of viable seeds Desert yellowhead produced. Seed metrics were analyzed with respect to population, treatment, year, and an interaction term between treatment and population (fixed effects). Year was analyzed as a categorical variable. We included a plant identification number as a random effect to explain variance within individuals. We also estimated the effect the pollen source had on seed mass and viability with a glm including population source of pollen, year and population with all hand-pollinated treatments in 2021 and 2022. P-values are non-trivial to calculate in mixed effects models, thus we used estimated marginal means (emmeans) to calculate p-values within factors (Lenth 2021).

We used glm to estimate differences in the number of ramets, total number of leaves, mean number of leaves per ramet, maximum leaf length, mean leaf length, number of flower stalks, number of flowers per stalk and total number of flowers in each hoop plot. We also used glm to estimated differences in the ratio of sexual to asexual reproduction between populations and years. We estimated what distribution best fit the data by examining histograms and using the fitdistrplus (Delignette-Muller and Dutang 2015). The number of seeds was analyzed with a normal distribution and all other variables were analyzed with a gamma distribution. All calculations and analyzes were done in Program R (R Core Team 2017) and data were summarized using the plyr package (Wickham 2011).

RESULTS

Climate data

Climate data differed between the populations of Desert yellowhead. Sand Draw received less precipitation compared to Cedar Rim ($t = 1.9$, $p = 0.06$; Fig. 4a) and 2021 was a drier year than 2022 ($t = 2.1$, $p = 0.04$). May was the wettest month ($t = 4.3$ – 6.6, $p < 0.001$; emmeans, $p < 0.0005$), and precipitation did not differ among the other months (emmeans, $p = 0.17$ -1.0). Percent soil water content was 4.3% higher at Sand Draw compared to Cedar Rim ($t = 6.1$, $p < 0.001$; Figs. 4b, c, d, e). Soil moisture content did not differ between years ($t = 0.73$, $p = 0.47$; Figs. 4f, g). The percent water content of the soil did not differ between areas adjacent to Desert yellowhead individuals (probe B) compared to those placed at least 30 cm away from individuals (probe A; $t = 0.73$, $p = 0.47$; Figs. 4b, c). May had the highest percent soil water content ($t = 7.6$ – 12.4, $p < 0.0001$; emmeans, $p < 0.0001$), and July was drier than August (emmeans, $p = 0.04$) and September (emmeans, $p = 0.08$). Percent soil water content measured by the short probes was 9.4% less compared to the long probes ($t = 18.9$, $t < 0.0001$).

Temperatures in May and June were colder in 2022 compared to the previous year. Mean air temperatures were 1.0°C warmer at Sand Draw compared to Cedar Rim ($t = 2.0$, $p = 0.15$; Figs 5a, b). The year 2021 was 1.0°C warmer on average than 2022 ($t = 5.1$, $p < 0.0001$). The mean air temperature varied among all months ($t = 6.3$ – 35.1, $p < 0.0001$; emmeans, $p < 0.001$; Fig. 5a, b) with July being the warmest month and May was the coolest. Maximum daily temperatures were 4.6°C warmer at Sand Draw than Cedar Rim ($t = 4.3$, $p = 0.02$) and 3.1°C warmer in 2021 compared to 2022 ($t = 7.7$, $p < 0.0001$). The daily maximum temperatures differed among all months ($t = 4.2$ – 16.4, $p < 0.001$) except June and September ($p = 0.14$; Fig. 5c, d). Minimum daily air temperatures were 1.4°C warmer at Cedar Rim ($t = 2.2$, $p = 0.11$), but minimum daily air temperatures did not differ between years ($t = 0.9$, $p = 0.36$). Minimum daily air temperatures differed among all months ($p = 8.9$ – 38.6, $p < 0.0008$; Fig. 5e, f).

Precipitation and temperature from the weather stations at Jeffrey City and Riverton differed from the stations within the Desert yellowhead populations. Up to 3x more precipitation was recorded within the Desert yellowhead populations compared to Riverton and >2x more compared to Jeffrey City (Fig. 6a). Mean air temperatures were slightly cooler at Jeffrey City compared to within the Desert yellowhead populations (Fig. 6b). Maximum air temperatures were up to 20°C cooler at Jeffrey City and Riverton compared to within the Desert yellowhead populations (Fig. 6c). Minimum air temperatures appeared to be similar among the locations with Riverton reporting the warmest minimums (Fig. 6d). We suggest that the weather stations at Jeffrey City and Riverton are not a reliable estimate of precipitation that Desert yellowhead plants are experiencing.

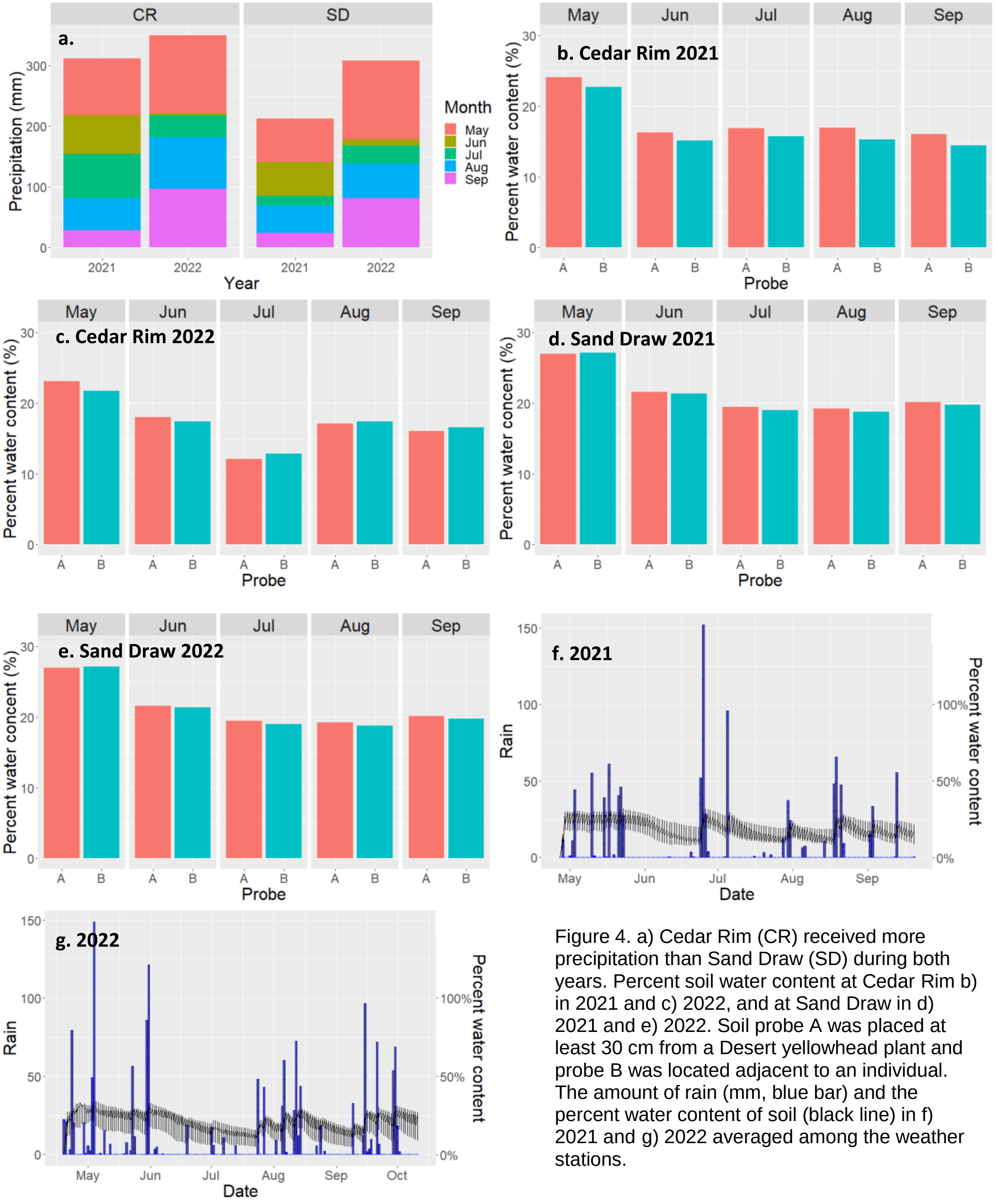
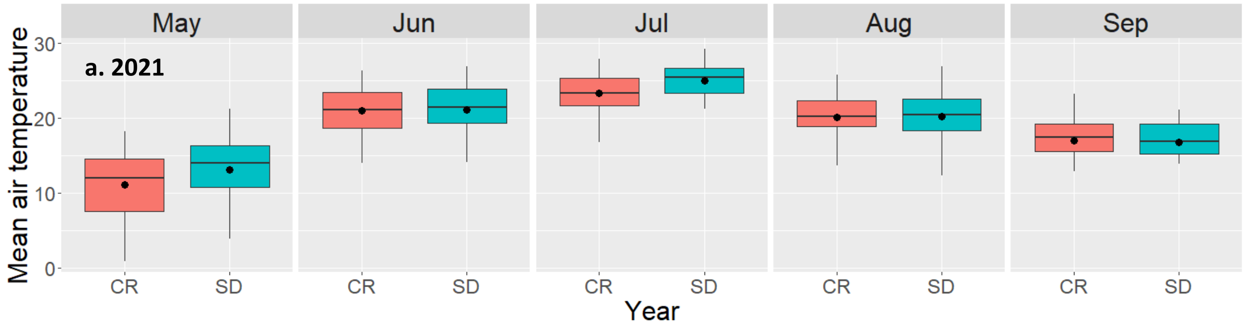


Figure 4. a) Cedar Rim (CR) received more precipitation than Sand Draw (SD) during both years. Percent soil water content at Cedar Rim b) in 2021 and c) 2022, and at Sand Draw in d) 2021 and e) 2022. Soil probe A was placed at least 30 cm from a Desert yellowhead plant and probe B was located adjacent to an individual. The amount of rain (mm, blue bar) and the percent water content of soil (black line) in f) 2021 and g) 2022 averaged among the weather stations.


a. 2021
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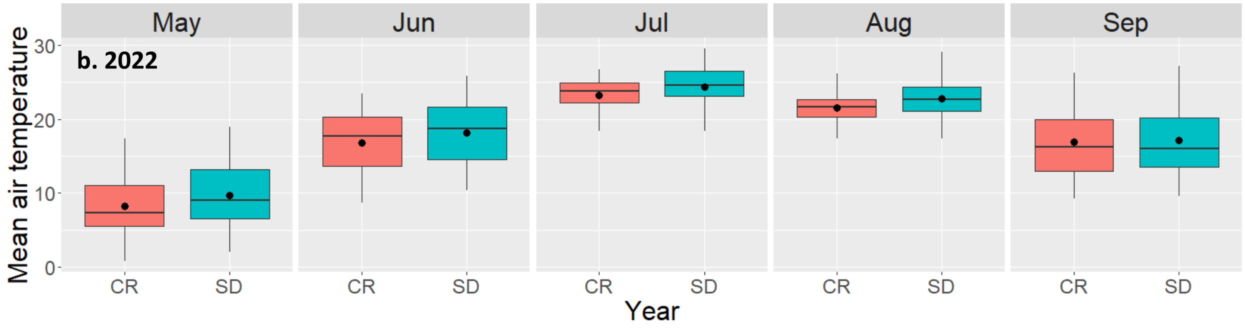
b. 2022
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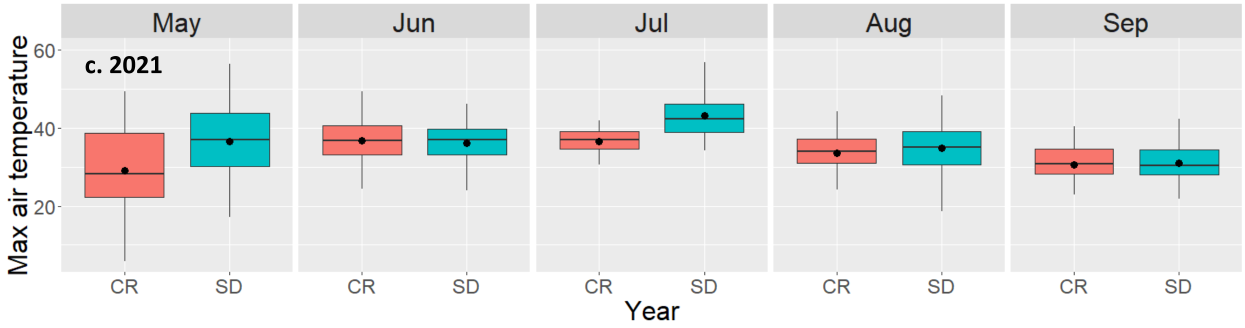
c. 2021
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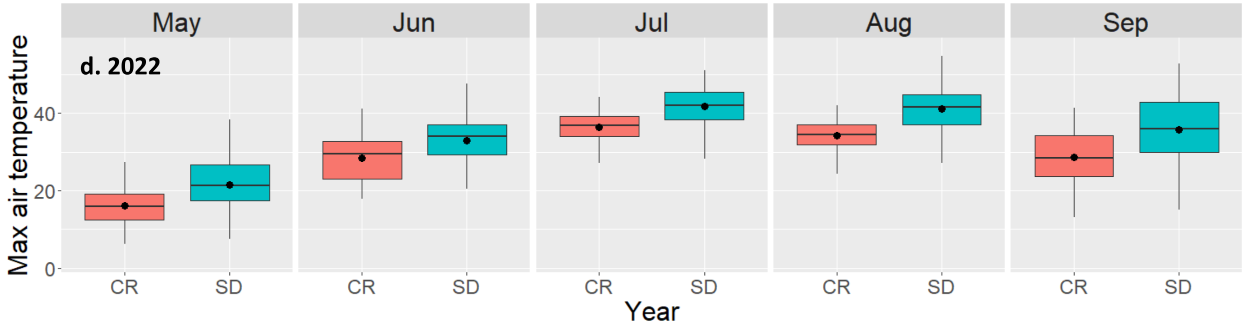
d. 2022
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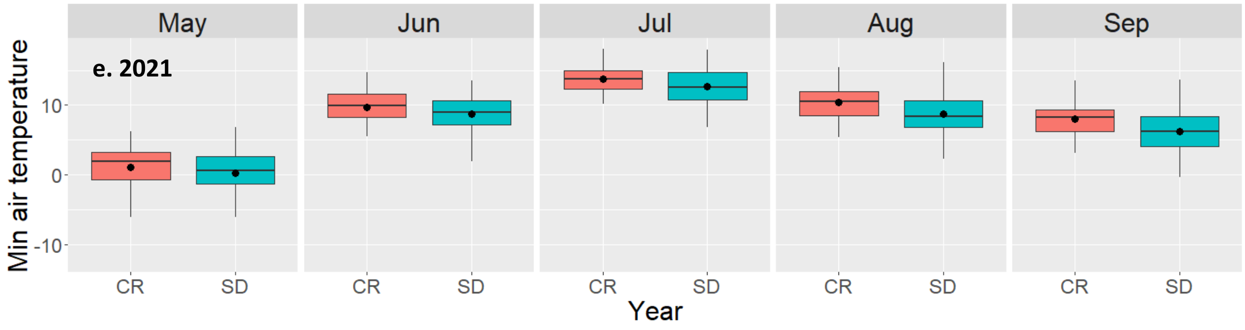
e. 2021
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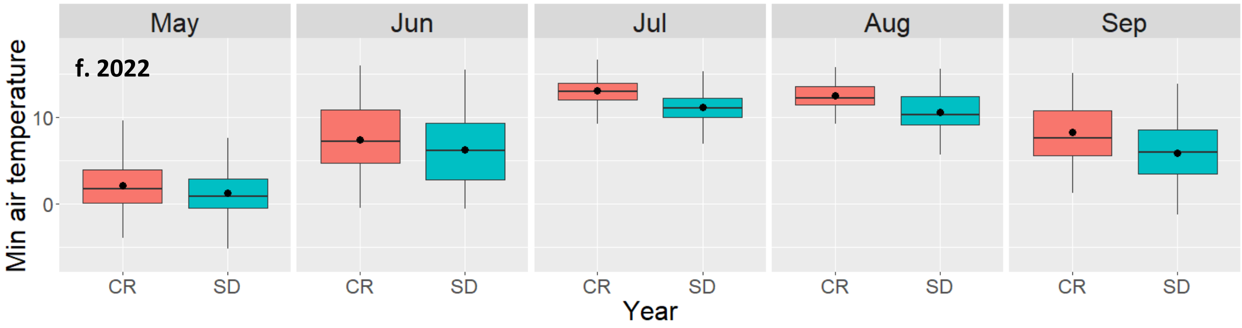

Figure 5. a) and b) Mean, c) and d) maximum, and e) and f) minimum daily temperatures by month at Cedar Rim (CR) and Sand Draw (SD). The year 2021 is show in a), c) and e), and 2022 is show in b), d) and f).

Figure 6. a) Precipitation, b) mean daily air temperature, c) maximum daily air temperature and d) miniumum daily air temperature within the Desert yellowhead populations (Cedar Rim and Sand Draw) compared to the nearest weather stations at Jeffrey City and Riverton, Wyoming. Values are reported during the growing season (May – September). Figures are made from monthly statistics.

Seed-set

The number of seeds produced by Desert yellowhead varied little among years, locations or treatments. Of the three years that seed production was measured for Desert yellowhead, 2018 produced the fewest seeds ($t = 1.8 – 3.2$; emmeans, $p = 0.01 – 0.17$; Fig. 7a). More seeds were produced at Cedar Rim than at Sand Draw ($t = 2.7$; emmeans, $p = 0.01$; Fig. 7b). The number of seeds produced among treatments did not vary ($t = 1.5 = 2.8$; emmeans, $p = 0.30 – 0.42$), except slightly fewer seeds were made in the hand-pollinated treatment compared to the bagged treatment (emmeans, $p = 0.02$; Fig. 7c). The number of seeds in the hand-pollinated treatment did not differ based on the population source of the pollen ($t = 0.4$, $p = 0.72$).

Pollen sourced from other plants was critical for Desert yellowhead to reproduce sexually and altered the mass of seeds. The mass of Desert yellowhead seeds varied among years, locations and treatments. Seeds were heaviest in 2018 and lightest in 2022 ($t = 6.7 – 9.9$; emmeans, $p < 0.0001 – 0.003$; Fig. 7d). The mass of seeds were 1.7x heavier at Sand Draw compared to Cedar Rim ($t = 5.4$; emmeans, $p < 0.0001$; Fig. 7e). Seeds produced in the bagged treatment were lighter than seeds produced from external pollen sources ($t = 3.7 – 5.2$; emmeans, $p < 0.0001 – 0.0006$; Fig. 7f). The mass of seeds produced in the open and hand-pollinated treatment did not differ (emmeans, $p = 0.28$) suggesting that pollinators did not limit the mass of seeds. The mass of seeds in the hand-pollinated treatment did not differ based on the population source of the pollen ($t = 0.5$, $p = 0.62$).

A low proportion of seeds produced by Desert yellowhead were viable in all years, locations and treatments. The lowest proportion of seeds were viable in 2022 ($t = 1.5 – 2.1$; emmeans, $p = 0.0008 – 0.09$; Fig. 8a). A higher proportion of seeds were viable at Sand Draw ($t = 3.0$; emmeans, $p = 0.003$; Fig. 8b) although the proportion of seeds that were viable in the open treatment was low overall (mean = 15% at Sand Draw across the 3 years). Most seeds in the bagged treatment were not viable and produced a smaller proportion of viable seeds than the hand-pollinated and open treatments ($t = 3.8 – 4.4$; emmeans, $p < 0.0001 – 0.0004$; Fig. 8c) suggesting that Desert yellowhead does not frequently produce viable seeds through self-pollination. The proportion of viable seeds in the open and hand-pollinated treatment did not differ (emmeans, $p = 0.82$) suggesting that pollinators did not limit viable seed production. The viability of seeds in the hand-pollinated treatment did not differ based on the population source of the pollen ($t = 0.8$, $p = 0.43$). Most seeds that we visually assessed as viable tested viable through Tetrazolium assays (Table 1). All seeds that we visually assessed as non-viable were non-viable according to Tetrazolium assays.

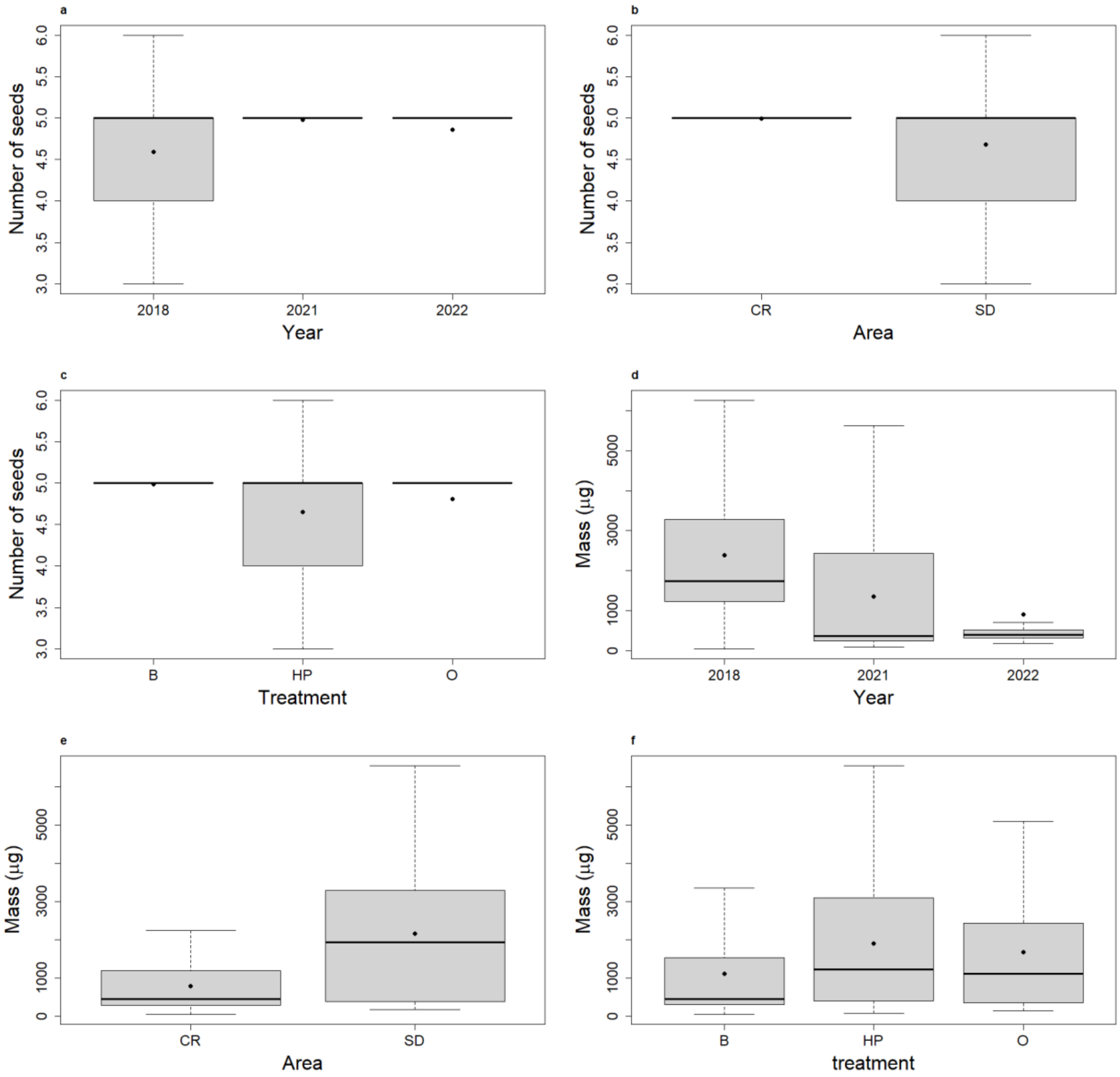

Figure 7. The number of seeds produced by Desert yellowhead was a) lowest in 2018, b) lower in the Sand Draw (SD) than Cedar Rim (CR) population and c) varied little among treatments. The mass of seeds was d) highest in 2018, e) highest at Sand Draw and f) higher in hand-pollinated (HP) and open (O) treatments compared to the bagged treatment (B; excluded pollinators). The mean is the black circle, the median is the bold line, the 25th and 75th percentiles are the lower and upper edges of the box, the whiskers show the minimum and maximum values excluding outliers. Outliers are not shown.

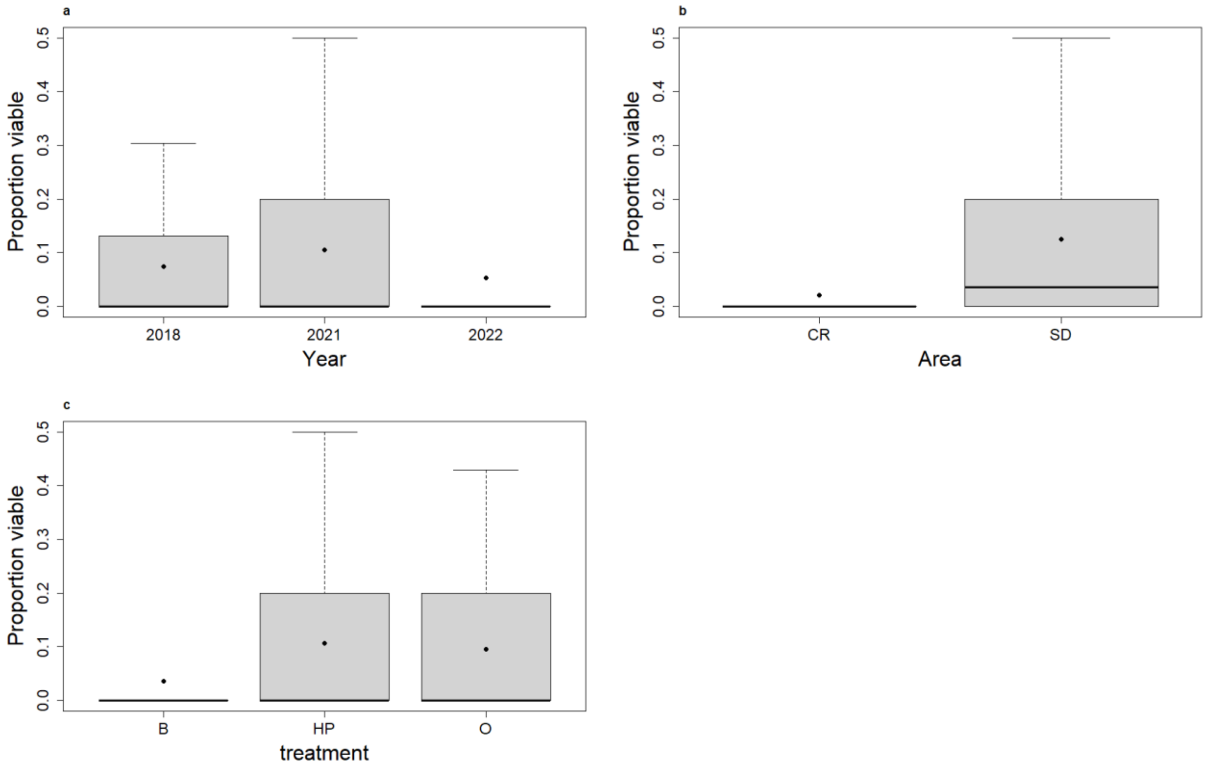

Figure 8. The proportion of viable seeds produced by Desert yellowhead was a) lowest in 2022, b) lower in the Cedar Rim (CR) than the Sand Draw (SD) population and c) higher in hand-pollinated (HP) and open (O) treatments compared to the bagged treatment (B; excluded pollinators). The mean is the black circle, the median is the bold line, the 25th and 75th percentiles are the lower and upper edges of the box, the whiskers show the minimum and maximum values excluding outliers. Outliers are not shown.

Table 1. We evaluated the accuracy of visual methods to assess seed viability and compared those to estimates from Tetrazolium assays.

		Tetrazolium test	
		Non-viable	Viable
Visual exam	Non-viable	100%	0%
	Viable	14%	86%

The seeds produced varied by temperature but not by precipitation. Desert yellowhead produced more seeds at higher maximum temperatures prior to blooming (May to July; $t = 4.0$, $p = 0.0001$; Fig. 9a), but precipitation, mean and minimum temperatures during this period did not alter seed mass ($t < 1.0$, $p > 0.15$). A higher proportion of viable seeds were produced at higher maximum temperatures between May and July ($t = 4.0$, $p < 0.0001$; Fig. 9b), but the proportion of viable seeds did not differ with precipitation ($t = 0.3$, $p = 0.79$). Our analysis compared two sites during two years which limited our analysis. More information is needed to assess under what climatic conditions Desert yellowhead produces the most seeds. Based on the limited data we have, Desert yellowhead may favor a maximum temperature measured at the soil level near 51°C during this time period, but more data are needed.

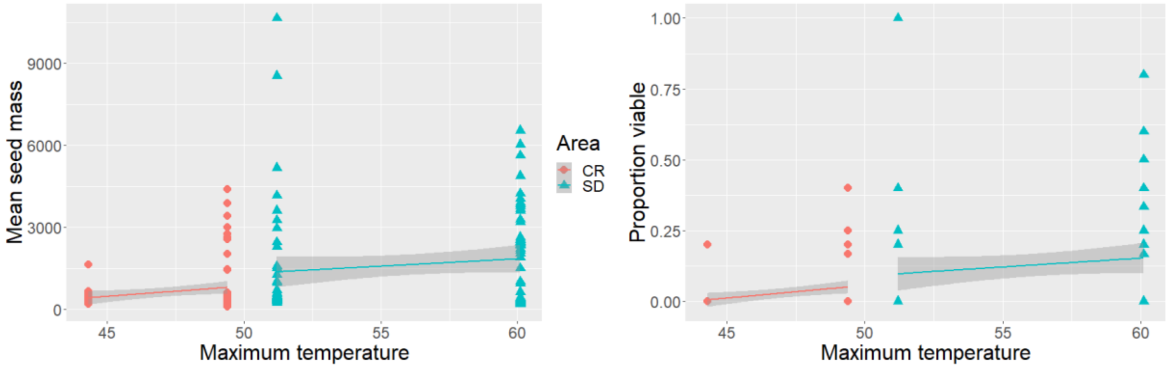

Figure 9. Desert yellowhead plants produced a) heavier seeds (µg) and b) a higher proportion of viable seeds at higher maximum temperatures between May and July based on two years of data. Individuals at Cedar Rim (CR) produced lighter and fewer viable seeds compared to Sand Draw (SD).

Ramets

Asexual reproduction through ramet development was higher in the Cedar Rim population. The number of ramets was slightly higher in August than June at Sand Draw (t = 2.0, p = 0.04; Fig. 10a). Plants at Cedar Rim produced 2x more ramets compared to individuals at Sand Draw (t = 2.8, p = 0.006, Fig. 10a). The number of ramets did not vary between years (t = 1.6, p = 0.12). The total number of ramet leaves within a hoop plot was higher at Cedar Rim compared to Sand Draw (t = 2.3, p = 0.02; Fig. 10b), but the total number of ramet leaves did not vary between June and August (t = 1.0, p = 0.31) or between years (t = 1.1, p = 0.27). The number of leaves per ramet did not differ among months (t = 1.7, p = 0.09), population (t = 0.88, p = 0.38; Fig. 10c) or year (t = 0.52, p = 0.60). The maximum leaf length on ramets did not vary among months (t = 0.78, p = 0.44), population (t = 0.26, p = 0.80) or year (t = 0.27, p = 0.79; Fig. 10d). The mean leaf length on ramets did not vary among months (t = 0.22, p = 0.76), population (t = 0.41, p = 0.32) or year (t = 0.78, p = 0.83; Fig. 10e).

The number of flower stalks (mean ± standard error; 1.4 ± 0.06) did not vary between population (t = 0.22, p = 0.83) or years (t = 0.14, p = 0.89). The mean number of flowerheads per stalk (58 ± 1.9) did not vary by population (t = 0.97, p = 0.34) or year (t = 1.5, p = 0.13). Finally, the total number of flowers within hoop plots (79 flowers ± 4.5) did not vary between population (t = 0.71, p = 0.48) or years (t = 1.3, p = 0.19).

Desert yellowhead individuals at Sand Draw appeared to spend more energy on producing seeds through sexual reproduction, while those at Cedar Rim put more resources into producing asexual ramets. The ratio of viable seeds to number of ramets was higher at Sand Draw compared to Cedar Rim (t = 7.5, p < 0.0001; Fig. 10f). The ratio was higher at Sand Draw from a combination of more viable seeds being produced and a lower number of ramets. Conversely, Cedar Rim produced few viable seeds and more ramets resulting in a lower ratio.

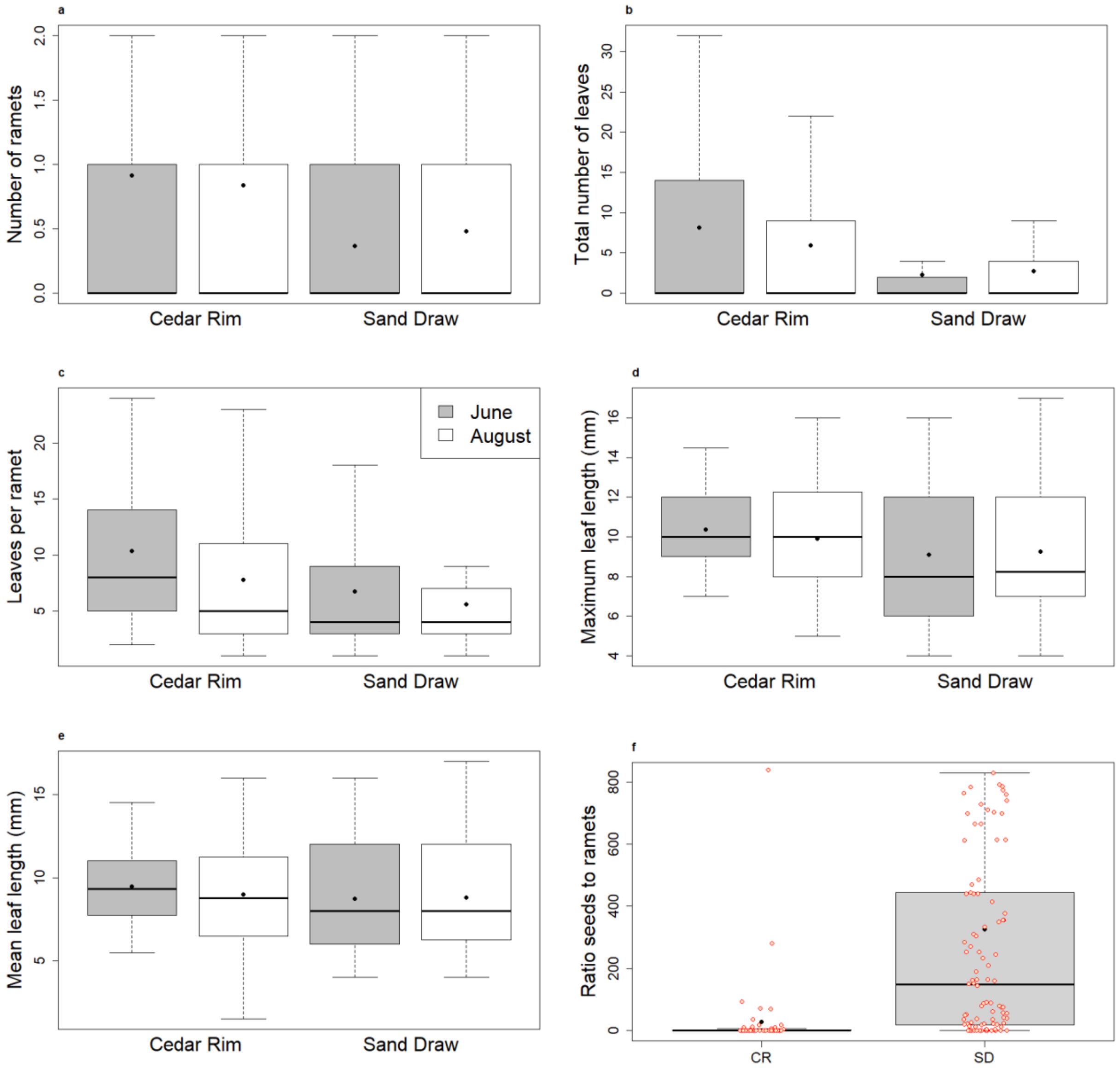

Figure 10. a) Twice as many ramets were produced at Cedar Rim compared to Sand Draw. b) We counted more leaves in each hoop plot at Cedar Rim than Sand Draw. c) The number of leaves per ramet, d) the maximum leaf length, and e) the mean leaf length did not differ by month or population. f) The ratio of viable seeds to ramets was higher at Sand Draw than Cedar Rim indicating that plants at Sand Draw invested more resources in seed production and individuals at Cedar Rim used more resources for ramet production. The mean is the black circle, the median is the bold line, the 25th and 75th percentiles are the lower and upper edges of the box, the whiskers show the minimum and maximum values excluding outliers. Outliers are not shown.

DISCUSSION

Desert yellowhead produced few viable seeds, especially in the Cedar Rim population. On average, 15% of seeds from Sand Draw and 1% of seeds from Cedar Rim were viable in the open treatment (ambient pollination) during 2018, 2021, and 2022. Seed viability in Desert yellowhead is much lower than reported for other rare species of Asteraceae. For example, up to 97% of seeds germinated for Viper's grass (*Scorzonera humilis*) in Luxembourg (Colling et al. 2004) and 31.4% of seeds were viable in Eared coneflower (*Rudbeckia auriculata*) in the southeastern US (Diamond et al. 2006). Seed viability may be lower in drier or colder environments due to harsher conditions; however, Asteraceae studies in such climates reported higher rates of viability than we measured. Two species from the Patagonian steppe, Solbrig's snakeweed (*Gutierrezia solbrigii*) and Slender ragwort (*Senecio subulatus*), produced 82% and 88% viable seeds, respectively (Masini et al. 2016). Seed viability in the open treatment was exceedingly low at Cedar Rim with zero viable seeds in 2018 (Handley and Tronstad 2021), 3.5% in 2021 and zero viable seeds in 2022. The production of few viable seeds suggests that Cedar Rim has less favorable conditions making ramet production a more cost effective option at this location. Seed viability was higher at Sand Draw (10 to 20% in the open treatment), but still lower than reported in other studies. Sand Draw likely has more favorable conditions for Desert yellowhead resulting in more sexual reproduction through seed production. Although Desert yellowhead can self-pollinate, plants produced few viable seeds through selfing. Most seeds are produced when pollinators transport pollen among plants thereby increasing genetic variation. Overall, the low percentage of seeds that are viable is concerning for the genetic diversity of the populations and for the perpetuation of the species, especially at Cedar Rim (Jabis et al. 2011).

Desert yellowhead produced more viable seeds during the warmer year and precipitation was not related to seed production. Desert yellowhead appeared to produce more seeds at warmer maximum temperatures and there is evidence that desert vegetation, particularly in cold deserts, may be more resilient to higher temperatures during the growing season (Lucas et al. 2008; Collins et al. 2010; Tielbörger and Salguero-Gómez 2014). Warmer temperatures can increase the productivity of some plants. For example, warmer nighttime temperatures were correlated with higher survival of Brenda's yellow cryptantha (*Cryptantha flava*) in Utah (Lucas et al. 2008) and increased cover of dominant species in the Chihuahuan Desert in New Mexico (Collins et al. 2010). Adaptations to high temperatures and variable precipitation may contribute to the resilience of Desert yellowhead to climate change; however, Desert yellowhead has limits as to how high of maximum temperatures it will thrive under. We need more data to understand the ideal temperature range for Desert yellowhead to produce viable seeds, and the influences of other biotic and abiotic factors.

Differences in data measured at our climate stations compared to weather stations in the nearest towns were likely due to local differences in climate and methods. We observed differences in precipitation between our study locations and the nearest weather stations. We also observed differences in precipitation between the populations. Despite the populations being ~8 km apart, Cedar Rim received more rain than Sand Draw during both years of our study. We attribute these differences to the highly localized nature of precipitation in Wyoming. Maximum temperatures were higher at our climate stations compared to the weather stations in the nearest towns. We attribute these differences to methods. Sensors at weather stations measure air temperature 1.5 m above the ground that are shaded (A. Bergantino, personal communication). Our sensors were placed on the ground which reflect temperature at the soil surface and reflect conditions that the plants are experiencing. Sensors placed at the ground level can measure warmer temperatures compared to those measured in the air due to heat accumulated by the soil and rocks (Robertson 1989).

Studying rare and endemic plants requires a delicate manner to conserve the species which can make scientific inquires more difficult due to limited sample sizes or restrictions to protect the species. We plan to halt Tetrazolium testing to measure seed viability because this technique damages seeds. We developed methods to visually inspect seeds to estimate viability based on the size, color, plumpness and overall appearance. By developing these non-destructive methods, we can return seeds to the Desert yellowhead populations and continue collecting data on seed viability. We did not measure any false negatives (seed visually appeared non-viable but Tetrazolium testing revealed it was viable; Fig. 11). Eighty-six percent of seeds appeared viable and tested positive for viability. Fourteen percent of seeds were false positives (seed visually appeared viable but Tetrazolium testing revealed it was non-viable). Knowing this information, we can correct our visual estimates of seed viability and return seeds to their respective populations.

Desert yellowhead plants at Cedar Rim experienced less soil moisture in the spring and more fluctuations in soil moisture during the summer. Cedar Rim received 45% more precipitation during the growing season in 2021 and 15% more in 2022 compared to Sand Draw. Interestingly, soil moisture was higher at Sand Draw and fluctuated less during the growing season. The soil moisture probes revealed more stable values at Sand Draw (standard deviation; sd = 5.5) compared to Cedar Rim (sd = 6.3) which reflects these differences. Although we did not measure snowpack, we observed larger snowbanks of stored moisture at Sand Draw compared to Cedar Rim. The snow melts into the shallow basin in spring and the basin shape retains the moisture in the soil throughout the heat of summer (Scott and Scott 2009). On the other hand, Desert yellowhead plants at Cedar Rim grow on the slopes of a rim with less potential to store snow.

Differing environmental factors between the Desert yellowhead populations produced varying ratios of sexual to asexual reproduction. The ratio of sexual to asexual reproduction in plants is negatively correlated (Herben et al. 2012) suggesting that plants only have so many resources that can be devoted to reproduction. Nectar volume and seed-set were negatively correlated with the number of stolons produced asexually in five species of Monkeyflower (*Mimulus*) grown in Utah (Sutherland and Vickery 1988). Plants may attempt to maximize their reproductive potential given their environment. For example, Narrowleaf peashrub had higher sexual reproductive output when conditions were less stressful (Wang et al. 2018). We hypothesize that Desert yellowhead is following a similar strategy. Despite the two populations producing a similar numbers of flowers, the proportion of viable seeds in the open treatments at Sand Draw was 5.5 times higher in 2021 and 9 times higher in 2022 compared to Cedar Rim. Sand Draw may have less stressful conditions compared to Cedar Rim allowing plants to direct more resources toward seed production. The shallow basin at Sand Draw accumulates snow which provides insulation in winter and maintains soil moisture during the summer likely contributing to more favorable conditions. Sand Draw may also have lower wind speeds which decreases evaporative water loss from the soil. The habitat at Sand Draw is more favorable for viable seed production and the plants there likely have more genetic diversity increasing biological fitness to confront changes in the environment (Agrawal 2001). Asexual reproduction is often favored in habitats with less ideal conditions and where sexual reproduction is less stable (Wang et al. 2018). Narrowleaf peashrub had higher asexual reproduction when conditions were more stressful (Wang et al. 2018) and plants at Cedar Rim appear to be responding similarly by producing twice as many ramets there compared to Sand Draw. Individual genetic combinations (clones) probably survive longer at Cedar Rim through ramet production, and asexual reproduction appeared to be exceedingly important to the persistence of Desert yellowhead in this population.

For plant species that are capable of sexual and asexual reproduction, allotting energy involves compromises (Vallejo-Marín et al. 2010; Lin et al. 2016; Wang et al. 2018). Asexual reproduction helps maintain a plant population in environments that may be marginal for the species or where sexual reproduction is too expensive or uncertain (Vallejo-Marín et al. 2010; Wang et al. 2018), such as Desert yellowhead at Cedar Rim. Populations can persist through asexual reproduction as long as the clones can endure changes in climate or perturbations (Vallejo-Marín et al. 2010). Because ramets are often produced close to the parent plant, they are more likely to be established in suitable habitat; however, the lack of genetic diversity in a population with a high percentage of clones reduces the protection against environmental change (Ellstrand and Elam 1993). More competition for resources may occur because ramets grow close to the parent. Population expansion and dispersal are much slower when asexual reproduction predominates. On the other hand, sexual reproduction provides more genetic combinations that give a population the diversity to endure many environmental circumstances (Jabis et al. 2011).

Seeds and pollen regularly disperse far from the parent plant possibly expanding the area of the population into new habitat more quickly. In fact, Desert yellowhead seeds are dispersed by the wind and seeds from the Sand Draw population may have established the Cedar Rim population (Heidel et al. 2011). In contrast, sexual reproduction requires more energy for the production of flowers, nectar, pollen and seed, especially in less favorable habitats (Kudo et al. 2008; Lin et al. 2016; Wang et al. 2018). Dispersed seeds also risk landing in less desirable conditions. Overall, sexual reproduction is the better option for plants in more suitable habitats while asexual reproduction is safer in less suitable habitats.

More knowledge is needed to address how plants are responding to climate and this need is even greater for rare and endemic plants whose risk of extinction is much higher (Flather and Sieg 2007). We demonstrated that a rare and endemic plant used different reproductive strategies in two populations that were only ~8 km apart. These contrasting strategies have consequences to the plant populations. We hypothesize that the population that dedicated more resources to sexual reproduction will persist longer in the face of climate change due to more genetic diversity. This population also has a higher potential to disperse to other areas and colonize as conditions change. On the other hand, we hypothesize that the population primarily maintained through asexual reproduction will persist in the short-term but will succumb to perturbations more readily due to less genetic diversity, less dispersal capability and because the habitat appeared less suitable. Both sexual and asexual reproduction are important to the continuance of Desert yellowhead, but the annual and long-term changes in climate will have different influences on the two types of reproduction. Given differences we observed in the populations of Desert yellowhead, we suggest that management decisions be considered for each population independently. With temperatures predicted to increase globally, asexual reproduction may predominate in many plant species causing a decrease in genetic diversity and dispersal leading to declines. Comparing sexual and asexual reproduction in rare and endemic plants can supply information about how populations are functioning, and provide insight about their potential persistence and resilience to future perturbations.

ACKNOWLEDGEMENTS

We thank Emma Freeland of the Bureau of Land Management, Wyoming, Lander Field Office for supporting this project and for her expertise, ideas and technical support. Bureau of Land Management technicians and interns: Katherine Bella, Natalie Wehner, Kristen Smith, Mia Farmer, Bella Norton, Rebecca Cross, and WYNDD technicians Katrina Cook and Amy Storey for technical support. We thank Megan Moss and Rodney Carter for providing accommodation. Gary Beauvais and Bonnie Heidel provided comments.

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