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Fire and Ungulate Herbivory Differentially Affect the Sexual
Reproduction of Generalist and Specialist Pollinated Plants

Andrew H. Lybbert

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of
Master of Science

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December 2014

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ABSTRACT

Fire and Ungulate Herbivory Differentially Affect the Sexual Reproduction of Generalist and Specialist Pollinated Plants

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Master of Science

Currently the size and frequency of wildfires are increasing at a global scale, including arid ecosystems that exhibit great sensitivity to disturbance. Fire effects on plant pollination and reproductive success in deserts are largely unknown. Plant dependence on animal pollinators for reproduction can increase the risk of reproductive failure if pollination services are hindered or lost. Species that depend on few taxonomically related pollinator species are expected to be most negatively affected by disturbances that disrupt pollination interactions.

To assess fire and isolation effects on reproductive success in desert plant communities, and how wildfire influences the pollination success of generalist and specialist pollinated plants, the number of flowers, fruits, and viable seeds produced by plants surviving in burned and unburned desert landscapes were compared. Fire increased flower production for wind and generalist pollinated plants, and did not affect specialist plant flower production. Increases may be associated with positive physiological responses exhibited by plants surviving in burned areas. Fire did not affect pollination services. Wildfire effects on fruit production were neutral or positive, and overall seed:ovule ratios varied by 3% or less in burned and unburned areas for each pollination strategy. Increasing isolation within burned areas did not affect fruit production for generalist or specialist pollinated plants, suggesting that pollination services are functional across expansive burned desert landscapes. Annual reproductive output varied between years in burned and unburned areas, and shifts likely resulted from variation in annual precipitation patterns. Reductions in landscape reproductive output may be partially compensated by increased per plant fruit and seed production and maintaining pollinator services across burned landscapes, providing native shrub communities the possibility to naturally recover from fire disturbances.

Habitat disturbances can influence plant interactions with herbivores, in addition to pollinators. To understand how fire and ungulate herbivory affect reproductive success of specialist pollinated desert plants, reproductive effort, floral herbivory, and pollinator visitation and success, were compared for *Yucca baccata*, and *Yucca brevifolia* in burned and unburned areas of the Mojave Desert. Fire increased *Y. baccata* flowering from 12% to 22% of plants in burned areas, but had no effect on the number of flowers or fruits produced per plant. Fruit set and pollinator collection failed at all sampled *Y. baccata* individuals, while fire and herbivory had no effect on *Y. brevifolia* flower, fruit, and pollinator collection. Herbivores consumed 50% and 67% of floral stalks produced by *Y. baccata* in unburned and burned areas. Herbivores pose a clear threat to successful sexual reproduction for *Y. baccata*. Removal of ungulate herbivores during important flowering periods may still result in failed fruit and seed production if local pollinator reserves have been drastically reduced or lost.

Keywords: fire, pollination, herbivory, flower production, fruit set, seed:ovule, Mojave Desert

ACKNOWLEDGEMENTS

I would like to acknowledge my advisor and committee for their guidance and support in completing this work. I would especially like to acknowledge Sam St. Clair whose vision, mentorship, and support facilitated the completion of this work, allowed me to discover my passion in research, and provided me tools to succeed as I move forward in my career. Thank you for believing in me, and providing me incredible opportunities. Special thanks to fellow graduate students Kevin Horn, Rory O'Connor, and Jason Bahr, whose friendship, support, and insights were valuable to me. This research required an incredible amount of data collection in the field, and sample analysis in the lab, and could not have been completed without an incredible group of undergraduate students, each of whom I consider a friend, and am grateful for. I would like to acknowledge, and express my love and thanks to my parents, who have always believed in my ability to accomplish more than I thought possible. Most importantly, I would like to express my love and appreciation to my incredible wife Virginia, and my beautiful daughter Elsie. Without their continual love, support, and encouragement I never could have completed this work. Lastly, I would like to express my thanks to Brigham Young University for providing me incredible educational opportunities, and the Monte L. Bean Life Science Museum for use of their fantastic field facility at the Lytle Ranch Preserve in southwestern Utah.

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Chapter 1: Fire increases post-fire reproductive success of wind, generalist, and specialist pollinated plants in the Mojave Desert, USA

Summary

Habitat disturbances that disrupt plant-pollinator interactions can drastically affect plant sexual reproductive success. Currently the size, frequency and severity of wildfires are increasing at a global scale, including arid ecosystems that exhibit great sensitivity to disturbance. Due to the historical infrequency of wildfire occurrence, fire effects on plant pollination and reproductive success in deserts are largely unknown. To assess the effects of fire on reproductive success in desert plant communities, and understand how wildfire influences the reproductive effort and pollination success of generalist and specialist pollinated species, we quantified and compared the number of flowers, fruits, and viable seeds produced by plants surviving in burned and unburned desert landscapes. Seven shrub species located in burned and unburned areas that utilize either wind, generalist, or specialist pollination strategies, were monitored over a three-year period to answer three primary questions: 1) how does fire disturbance affect flower, fruit, and seed production differentially in wind, generalist, and specialist pollinated species? 2) Does increasing isolation within burned desert landscapes decrease pollination efficiency and fruit set? 3) Do fire effects on plant reproduction vary between years? Fire increased flower production for wind and generalist pollinated plants, and did not affect specialist plant flower production. Such increases may be associated with positive physiological responses that surviving plants exhibit in areas burned by wildfire. Pollination success, measured as fruit set and seed:ovule ratios, was generally unaffected by fire. Fire increased, or had no effect, on fruit production across pollination strategies, and overall seed:ovule ratios varied by 3% or less between burned and unburned areas for each pollination

strategy. Increasing isolation within burned areas did not affect fruit production for generalist or specialist pollinated plants. Successful pollination along burned edges, and in isolated burned areas, suggests that pollination services are functional across burned desert landscapes. Annual flower, fruit, and seed:ovule ratios varied between years in burned and unburned areas. Yearly shifts in reproduction likely resulted from variation in annual precipitation patterns. Reductions in landscape reproductive output may be partially compensated by increased per plant fruit and seed production by maintaining pollinator services across burned landscapes, and providing native shrub communities the opportunity to naturally recover from fire disturbances.

1. Introduction

The vast majority of flowering plant species depend on animal pollinators to facilitate successful pollination and sexual reproduction (Renner 1998). Although animal pollen vectors increase the efficiency of pollen transfer between flowers, dependence on mutualists for reproduction can increase plant susceptibility to habitat disturbances that disrupt plant-pollinator interactions (Bond 1994; Aizen et al. 2002). Contrasting disturbance effects on plant sexual reproduction may be explained by differences in mating system and pollinator dependencies (Bond 1994; Aizen and Feinsinger 2002). Self-incompatible (SI) plants can only produce seeds by receiving outcrossed pollen from other individuals, whereas, self-compatible (SC) species are able to sexually reproduce through autonomous, within-flower selfing (Lloyd 1992; Richards 1997). Generalist (G) pollinated plants receive pollen from several or many taxonomically diverse species, whereas specialist (S) depend on as little as one or a few taxonomically related pollinators (Bond 1994; Waser et al. 1996).

If reproductive success is related to plant dependence on pollination mutualism, self-incompatible, specialist pollinated plants should be most at risk, and display greater reproductive failure to habitat disturbances than generalist, self-compatible species (Bond 1994; Waser et al. 1996). Recent reviews indicate that habitat disturbances have considerable negative effects on both generalist and specialist pollinators, and suggest that no generalizations can be made about plant susceptibility to disturbances based on breeding system and pollination specialization (Aizen et al. 2002; Aguilar et al. 2006). However, the majority of these comparisons did not include multi-year, multi-species, or highly specialized, self-incompatible species (e.g., yucca-yucca moth).

Habitat disturbances can engender strong negative effects on the reproductive responses of plant species (Aguilar et al. 2006), but may also potentially improve the quality of pollen transfer by altering pollinator movement in ways that increase outcrossing (Dick 2008). Successful pollination is influenced by many interacting factors including the number of, and distance between flowers and pollinators (Ghazoul 2005; Kremen et al. 2007). Reduction in population size, or increased isolation between plants, enhances the risk of pollination failure, reduced reproductive success, and local extinction (Jennersten 1988; Saunders et al. 1991; Kunin 1997). Direct reductions in plant density, pollinator density, and pollinator foraging behavior (Hadley and Betts 2012) can increase the risk of reproductive failure through mechanisms of pollen limitation, and inbreeding depression (Saunders et al. 1991; Kearns and Inouye 1997; Jennersten 1988; Lennartsson 2002).

Currently fire size and frequency are increasing at a global scale (Bowman et al. 2011; Neary et al. 1999; Pyne et al. 1996; Brooks et al. 2004), a trend that is expected to increase under

future climate conditions (Westerling et al. 2006). Understanding fire effects on plant pollination and reproductive success will be imperative to mitigating negative impacts, and facilitating recovery in burned landscapes. The net overall effect of fire on plant sexual reproduction is influenced by a combination of negative and positive effects. Plants can be positively affected by fire (Kerstyn and Stiling 1999) through reductions in competition, resource pulses, increased reproductive vigor (Brewer and Platt 1994) and reduced pathogen loads (Waldrop et al 1992; Kerstyn and Stiling 1999). However, if surviving plants become isolated from pollinating vectors, plant fitness may be negatively affected via pollen competition, increased selfing events, or pollination failure (Kearns and Inouye 1997).

Fire regimes across the warm deserts of the American southwest have shifted drastically in recent years. Fire frequency and size have increased substantially in the Mojave (Brooks and Matchett 2006), Sonoran (Brown 1994; Allen 2007) and Great Basin Deserts (Epanchin-Niell et al. 2009; Haubensak et al. 2009; Bukowski and Baker 2013). Shifts are strongly linked to exotic annual plant invasions that produce fine fuels that carry fire between native shrubs across desert landscapes (Brooks et al. 2004). Due to the historical infrequency of fire disturbances across these regions, desert plant communities generally experience high fire mortality (Brooks and Minnich 2006). The number of species that re-sprout from roots are limited, seed banks may be compromised, and recovery is slow (Webb 2002; Esque 2004; Abella 2009; Abella et al. 2009). This poor adaptability, coupled with unsuccessful and expensive rehabilitation strategies, suggests that native plant community re-establishment will be heavily dependent on the production and dispersal of propagules into fire fragmented spaces from surviving plants or small unburned vegetation patches within burned desert landscapes (Kay and Graves 1983; Walker and Powell 1999; Epanchin-Niell et al. 2009). As the frequency and size of fires

increase, successful pollination across desert landscapes may become increasingly difficult if isolation reduces plant reproductive success, or leads to local plant extinctions. Although desert shrub communities are becoming increasingly exposed to fire disturbances (Brooks and Matchett 2006), analysis of plant sexual reproduction across desert biomes have not been completed.

To assess the effects of fire on plant reproductive success in a desert biome, and understand how wildfire influences pollination success as a function of pollination strategy, and increased plant isolation, we quantified and compared the number of flowers, fruits, and viable seeds produced by plants in burned and unburned desert landscapes. These data were collected from seven shrub species over a three-year period. Selected species ranged in pollinator dependence from zero dependency wind pollinated species, to a plant pollinated by a single insect species. Data were collected to answer three primary questions: 1) how does fire disturbance affect flower, fruit, and seed production differentially in wind, generalist, and specialist pollinated species? 2) Does increasing isolation within burned desert landscapes decrease pollination efficiency and fruit set? 3) Do fire effects on plant reproduction vary between years?

2. Methods

2.1 Site location and description

This study was conducted in the Beaver Dam Wash of southwestern Utah during three successive spring flowering periods (March-June) from 2012-2014. This area is located in the northeastern region of the Mojave Desert, which is generally characterized by widely spaced, low growing perennial shrubs (Cody 1986a, 1986b). The dominant flora consists of blackbrush

(*Coleogyne ramosissima*), creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and Joshua tree (*Yucca brevifolia*). In recent years the landscape has been altered by plant invasions and changing fire regimes. Invasive plant species including red-stem filaree (*Erodium cicutarium*), Schismus spp. and red brome (*Bromus rubens*). Flower and fruit counts from burned areas were sampled from four individual fires that occurred in the spring and summer of 2005: Westside (June, 27,059 ha), Duzak (July, 7,065 ha – within Utah), Burgess 1 (July, 60 ha), and Burgess 2 (July, 712 ha) (Utah Bureau of Land Management). Weather data was taken from the MesoWest Badger Spring (BADU1) weather station (mesowest.utah.edu), located within the Beaver Dam Wash study area (37.1506° N, 113.9539° W, elevation: 1216 m).

2.2 Study Species

To understand fire effect on desert plant reproduction we selected seven native perennial desert shrub species that are not only prevalent across the Mojave Desert, but also represent a range of breeding system characteristics and pollinator dependency (Table 1.1).

(1) *Ambrosia dumosa* (Gray) Payne (burrobush, hereafter referred to as ‘*Ambrosia*’) is a wind-pollinated, drought-deciduous rhizomatous shrub growing from 20-60 cm tall. It flowers anytime during the spring, summer, and fall, depending on precipitation patterns (Ackerman et al. 1980).

(2) *Coleogyne ramosissima* Torr. (blackbrush, hereafter referred to as ‘*Coleogyne*’) is a wind pollinated rounded shrub, 30-120 cm or more tall (Welsh et al. 1993), that dominates much of the landscapes throughout its range. Flowering occurs from late March – early May (Bowns and West 1976). However, the degree, and timing of flowering varies significantly from year to year (Beatley 1974).

(3) *Larrea tridentata* (DC.) Coville (creosote bush, hereafter referred to as ‘*Larrea*’) is a drought-tolerant, evergreen shrub that typically grows 50-200cm tall, but can reach heights up to 400 cm (Munz and Keck 1959). *Larrea* boasts a rich pollination guild, which consists of >100 pollinator species (Minckley et al. 1999).

(4) *Encelia farinosa* A. Gray ex Torr. (brittlebush, hereafter referred to as ‘*Encelia*’) is a drought-deciduous shrub that grows to about 150 cm (Monson et al. 1992), and flowers from March-May (Munz and Keck 1968). *Encelia* flowers are visited by a wide variety of bee and beetle species, however, known pollinators are not well established in the primary literature, and were therefore determined using the discover life database (discoverlife.org).

(5) *Thamnosma montana* Torr. & Frém. (turpentine broom, hereafter referred to as ‘*Thamnosma*’) is a profusely branched, 30-80 cm tall, deciduous shrub (Benson and Darrow 1981). Spring flowering is variable, beginning as early as February, or starting late enough to extend into May (Kearney et al. 1960; Munz 1974). *Thamnosma* flowers are visited by bees and butterfly species, however, visitors are not well established in the literature, and were therefore determined using the discover life database (discoverlife.org), and personal observations.

(6) *Krameria grayi* (Rose & Painter) (white ratany, hereafter referred to as ‘*Krameria*’) is a densely branched, deciduous shrub 30-60 cm tall. *Krameria* was categorized as a specialist pollinated plant because the flowers offer oil, rather than nectar rewards to flower visiting insects, which restricts *Krameria* visitation to bees primarily in the genus *Centris* (Buchmann 1987).

(7) *Yucca brevifolia* Engelm. (Joshua tree, hereafter referred to as ‘*Yucca*’) is a tall, evergreen, tree-like plant. Size and growth form often vary with site and climate conditions (Munz 1974). Flowers occur in dense, heavy panicles (Hickman 1993). *Yucca* represents the most specialized pollination strategy in this study. Seed production is periodic or rare, although wet years are suggested as best for flowering and fruit production (Maxwell 1971).

2.3 Study design

To survey plant reproductive responses to fire over the three year study period we established a network of 1 kilometer transects by driving small metal posts into the ground to act as permanent markers every 100m along the full length of each transect (0m, 100m, 200m and so on). Each transect in a pair was positioned in a burned or unburned area, and each transect was positioned approximately 200m on either side of a burn boundary. For the 2012 data collection five transect pairs were positioned along adjacent burned/unburned boundaries incorporating four independent fires that occurred in 2005 (Fig. 1.1). For the 2013 and 2014 field seasons an additional burned/unburned transect was established; and 5 transects were set up within the burns in which sampling points were on average > 1.5 km from burn boundaries (isolated burned) to test the effects of isolation within large fires on plant reproductive success. GPS waypoints were taken so each marker could be repeatedly located throughout the duration of our study. Many of the study species flowered episodically from year to year, which is why some species were not sampled in each field season. In 2012 data were collected from four species (*Ambrosia*, *Larrea*, *Encelia*, and *Krameria* fruit counts). All seven species were sampled in 2013 (Table 1.1). In 2014 five species were sampled (*Ambrosia*, *Larrea*, *Encelia*, *Thamnosma*, and *Krameria*).

To determine individual plants for monitoring, we selected an individual of each species in closest proximity to each 200m increment marker along all transects (5 plants/species/transect). To limit selection bias, plants were chosen before any flowering had occurred. Some species were not evenly represented across all sample areas. *Ambrosia*, *Coleogyne*, and *Krameria* were particularly difficult to locate in the 5 isolated expansive burned transects, resulting in their exclusion from evaluation in these areas. Individual plants were marked with a specific rounded aluminum numerical identification tag and a GPS waypoint was taken so we could repeatedly monitor the same individuals and capture the variation of our reproductive response variables throughout the duration of the study.

To account for variation in plant size, the height and the width along major and minor perpendicular axes was used to calculate the volume of each plant. *Ambrosia*, *Coleogyne*, *Thamnosma*, and *Krameria* volumes were calculated based on the shape of an oblate spheroid, *Encelia* volumes were calculated based on the shape of a half spheroid, and *Larrea* and *Yucca* volumes were calculated based on the shape of a cone with an elliptical cross section.

2.4 Flower and fruit counts

Flowers on many of our study species can bloom and wilt over a very short period of time making accurate total seasonal flower counts for all species and transects logistically impossible. For that reason mean flower counts were generated by averaging only the single largest flower count recorded for each plant within each year, so they do not represent total average flower production for the season, unlike the mean fruit counts.

Flowers, and fruits were counted on every plant selected along each transect. Flower counts were conducted every other week throughout the duration of the spring flowering period (March-June) until it was clear that peak flowering had passed. Fruit counts were completed 2-3 weeks after flowering had ceased. Flower and fruit counts per plant were exhaustive in 2012, however, in 2013 and 2014 counts were estimated by multiplying counts of randomly chosen quadrants. To accurately count flowers that are displayed in tightly packed clumps or inflorescences, we generated an average flower number/inflorescence by collecting 10 inflorescences from several adjacent individuals in each of the three landscape categories (unburned, burned edges, and isolated burned) and carefully counted the number of flowers in them. Total flower counts were then estimated by multiplying the average flower number per inflorescence by the total number of inflorescences counted on the plant. This method was used only for flower counts on *Ambrosia* and *Yucca* individuals. Fruit sizes for these taxa were large and distinct enough to be counted individually. In the first year that *Krameria* and *Thamnosma* were added to the study, there were no flower counts because we added them too late in the field season to accurately count flowers.

Flower and fruit production per unit ground area was estimated by multiplying plant densities by average flower and fruit production per plant. Plant community structure was characterized using circular vegetation plots with a 5m radius placed every 100m along each of our transect lines for a total of 169 plots (70 unburned, 69 burned edges, and 50 isolated burned). Within each plot, shrubs were counted, identified, and plant height, as well as major and minor axes, were measured. Plant species densities were used to calculate the number of species individuals per hectare in unburned, burned edges and isolated burned areas. Landscape level reproductive responses were estimated by multiplying the number of species individuals per

hectare with the mean number of flowers and fruits produced per plant calculated for each species within each respective burn type and year. Plants in the vegetation plots with volumetric measurements which fell below that of the smallest plants used to sample flower and fruit count data, were assumed reproductively immature, and were excluded from calculations.

2.5 Seed:ovule ratios

Fruits were collected after maturing on the plant (approximately 1-2 months), from the same individuals where flower and fruit counts were completed, and came from multiple shrubs along each transect. The *Ambrosia*, *Larrea*, *Encelia*, and *Krameria* species were evaluated in 2012 and 2013, with the addition of the *Yucca* species in 2013 (the only year in which it flowered during our study). Fruits were collected into paper coin envelopes, placed into brown paper bags, and stored in a dry, cool, dark location in the St. Clair research lab in Provo, UT. Ovules were evaluated based on size, color, shape and firmness, after careful extraction from other protective tissues on the fruit. An ovule was considered a filled seed if it was full size, dark, and hardened when prodded with a dissecting needle.

2.6 Statistical analysis

Mixed-effects linear models were used to examine fire effects on flower, fruit, plant density and percent cover, and seed:ovule proportions using Automatic Differentiation Model Builder (glmmADMB). ADMB fits mixed effects models to count data using Poisson or negative binomial response distributions (Skaug et al. 2011). In our mixed-effect models burn type, pollination strategy, and year were specified as fixed effects, site (transect number) and plant size (volume) were specified as random effects, and the specific plant identification number was examined as a random effect in comparisons between years to account for repeated measures.

Flower, fruit, and vegetation data were evaluated using a negative binomial distribution, and seed:ovule ratios were evaluated using a binomial distribution due to the binary response (filled = 1, aborted = 0). To verify the application of a negative binomial distribution, assumptions of normality and homoscedasticity were visually inspected using residual plots (e.g. histogram, scatterplot, and qqnorm of residuals). The negative binomial distribution fits biological count data well, and provides greater flexibility in evaluating a variety of patterns in animal or plant distributions (White and Bennetts 1996). All calculations, models, assumption analyses and determinations of statistical significance were performed using program R software language and environment for statistical computing (R Development Core Team 2008).

3. Results

3.1 Fire effects on shrub flower, fruit, and seed production

Fire effects on shrub flower production were neutral to positive across species and pollination groups. Fire more than doubled flower production in burned edge areas for wind pollinated plants (Fig. 1.2) Among wind pollinated plants, *Ambrosia* flower production increased more than four fold in burned edge areas in 2012 (Table 1.2). Fire effects on *Ambrosia* and *Coleogyne* flower production were neutral in 2013 and 2014 (Table 1.2). Overall, fire effects more than doubled flower production in burned edge areas for generalist pollinated plants, increasing 2.6 fold (Fig. 1.2, Table 1.2). Among pollination generalists, *Larrea* flower production increased more than three fold in 2012 and 2014, and more than two fold in 2013 (Table 1.2). Fire effects on *Encelia* flower production were neutral in all three study years (Table 1.2). Fire increased *Thamnosma* flower production 2.7 fold in burned edge areas (Table 1.2). Fire

effects on flower production were neutral for specialist pollinated plants overall, and at the individual species level for both *Krameria* and *Yucca* (Table 1.2).

Fire effects on shrub fruit production were neutral to positive across species and pollination groups, with the exception of *Encelia* 2013. Fire effects on fruit production were neutral for wind pollinated plants overall (Fig. 1.2). Among wind pollinated plants, *Ambrosia* fruit production increased 10 fold in burned edge areas in 2012 (Table 1.2). Fire effects on *Ambrosia* and *Coleogyne* fruit production were neutral in 2013 and 2014 (Table 1.2). Overall, fruit set for generalist pollinated plants increased 2.6 fold in burned edge areas (Fig. 1.2). Among generalist pollinated plants, fruit production for *Larrea* increased 4.7 fold in 2012, but effects were neutral in 2013 and 2014 (Table 1.2). Fire reduced *Encelia* fruit production in burned edge areas 9.8 fold in 2013, but effects were neutral in 2012 and 2014 (Table 1.2). Fire increased *Thamnosma* fruit production in burned edge areas 2.9 and 4.9 fold in 2013 and 2014 (Table 1.2). Overall, fire effects on fruit production were neutral for specialist pollinated plants, and at the individual species level for both *Krameria* and *Yucca* (Table 1.2).

Fire affected shrub seed:ovule ratios differently across pollination strategies (Fig. 1.2). Overall, fire had no effect on seed:ovule ratios of wind pollinated plants, with only about 1% of fruits producing filled seeds (Fig. 1.2). Among wind pollinated plants, fire had no effect on *Ambrosia* seed production in 2012 or 2013 (Table 1.2). Fire reduced seed:ovule ratios from 53% to 50% in burned edge areas for generalist pollinated plants (Fig. 1.2). Among generalist pollinated plants, fire decreased *Larrea* seed:ovule ratios from 79% to 73% in burned edge areas in 2012 (Table 1.2). In 2013 fire increased *Larrea* seed:ovule ratios 3.6 fold, from 10% to 36% in burned edge areas (Table 1.2). Fire effects on *Encelia* seed:ovule ratios were neutral in 2012,

and positive in 2013, increasing seed:ovule ratios from 21% to 29% (Table 1.2). Specialist pollinated species produced the highest number of seeds per ovule overall, and fire only slightly increased seed production in burned edge areas from 64% to 65% (Fig. 1.2). Among specialist pollinated plants, fire had no effect on *Krameria* seed production in 2012 or 2013, and all recorded seed:ovule ratios fell below 10% filled seed (Table 1.2). Fire decreased seed:ovule ratios 5% for *Yucca*, dropping from 72% to 67% in burned edge areas (Table 1.2).

3.2 Isolation effects on pollination efficiency in burned landscapes

Isolation effects on shrub floral production were neutral for generalist and specialist pollinated plants when compared to burned edge locations. Overall, isolation had no effect on generalist pollinated plant flower production (Fig. 1.2). Among generalist pollinated plants, isolation effects were neutral for *Larrea*, *Encelia*, and *Thamnosma* in 2013 and 2014 (Table 1.2). Isolation did not affect specialist flower production between isolated burned locations, and burned areas situated adjacent to fire boundaries (Fig. 1.2). However, due to the absence of *Krameria* individuals in isolated burned areas, only *Yucca* values were used for specialist burned edge-isolated burn comparisons.

Isolation effects on shrub fruit production were neutral for generalist and specialist pollinated plants when compared to burned edge locations. Overall, isolation had no effect on generalist pollinated plant fruit production (Fig. 1.2). Among generalist pollinated plants, isolation effects were neutral for *Larrea*, *Encelia*, and *Thamnosma* in 2013 and 2014 (Table 1.2). Isolation had no effect on fruit set for specialist pollinated plants when compared to burned edge areas (Fig. 1.2). Due to the absence of *Krameria* individuals in isolated burned areas, only *Yucca* values were used for specialist burned edge-isolated burn comparisons.

3.3 Annual fluctuations in flower, fruit, and seed:ovule ratios by species

Shrub flower, fruit and seed:ovule ratios varied drastically by year and burn type. Annual fluctuation had no effect on flower production in unburned areas between all species and year comparisons (Table 1.4). *Ambrosia* flower production in burned edge areas increased 49% from 2012 to 2013, but dropped 90% from 2013 to 2014 (Table 1.4). *Larrea* flower production in burned edge areas increased 65% from 2012 to 2013, and did not fluctuate significantly from 2013 to 2014 (Table 1.4). *Encelia* flower production in burned edge areas increased 200% from 2012 to 2013, and did not fluctuate significantly from 2013 to 2014 (Table 1.4). *Krameria* flower production, which was only recorded in 2013 and 2014, decreased 93% in burned edge areas from 2013 to 2014 (Table 1.4).

Ambrosia fruit production increased substantially in both unburned and burned edge areas, increasing 605% and 874 % from 2012 to 2013 (Table 1.4). *Ambrosia* fruit production did not fluctuate between 2013 and 2014 in unburned or burned edge areas (Table 1.4). *Larrea* fruit production did not fluctuate significantly in unburned or burned edge areas across study years (Table 1.4). Annual variation in *Encelia* fruit production varied between unburned and burned edge areas. *Encelia* fruit production in unburned areas increased 456% from 2012 to 2013, but did not fluctuate significantly from 2013 to 2014 (Table 1.4). *Encelia* fruit production in burned edge areas decreased 72% from 2012 to 2013, but did not fluctuate significantly from 2013 to 2014 (Table 1.4). Annual variation in *Krameria* fruit production varied between unburned and burned edge areas. In unburned areas *Krameria* fruit production did not vary between years (Table 1.4). In burned edge areas *Krameria* fruit production decreased 79% from 2012 to 2013, but did not fluctuate significantly from 2013 to 2014 (Table 1.4).

3.4 Fire effects on species reproduction at the landscape scale

Fire effects on plant density and percent cover were neutral or negative for all seven study species. In burned edge locations, fire significantly reduced plant density for five of the seven study species (Table 1.5). In isolated burned locations, vegetation analysis failed to detect the presence of surviving *Ambrosia*, *Coleogyne*, and *Krameria* individuals. *Larrea* density in isolated burned areas was reduced compared to both unburned and burned edge locations (Table 1.5). *Thamnosma* density was reduced compared to unburned areas, but was slightly higher compared to burned edge locations (Table 1.5). *Yucca* density in isolated burned locations was slightly higher than burned edge locations, and did not differ significantly from unburned areas (Table 1.5). Fire reduction of plant cover in burned edge locations was significant for six of the seven study species (Table 1.5). *Larrea*, *Encelia*, and *Yucca* percent cover in isolated burned areas did not differ significantly from unburned or burned edge locations (Table 1.5). *Thamnosma* percent cover in isolated burned locations increased slightly compared to burned edge locations and was not different for unburned areas (Table 1.5).

In conjunction with reductions in plant density and cover, fire drastically reduced the total predicted number of flowers and fruits produced across unburned and burned landscapes (Table 1.5). Conspecific reductions in flower production per unit ground area in burned edge locations ranged from 30% to 98%, with the exception of *Encelia* flower production (Table 1.5). Fruit production per unit ground area reductions ranged from 31% to 97% in burned edge locations (Table 1.5). In isolated burned areas no surviving individuals were recorded for *Ambrosia*, *Coleogyne*, or *Krameria* (Table 1.5). Of the species that could be located in isolated burned areas, flower reductions per unit ground area ranged from 57% to 91% (Table 1.5). Fruit

reduction per unit ground area in isolated burned areas ranged from 91% to 96%, with the exception of *Thamnosma* fruit production (Table 1.5).

4. Discussion

4.1 Fire effect on flower production

Fire strongly increased flower production for wind and generalist pollinated plants in burned edge areas, and had no effect on specialist pollinated plant flower production (Fig. 1.2, Table 1.2). Positive fire disturbance effects on plant reproduction have been reported in the literature, and are not uncommon, in fire driven/dependent ecosystems (Brewer and Platt 1994; Kerstyn and Stiling 1999; Barrios et al. 2011). However, the strong positive effect of fire on flower production in desert shrub species is particularly interesting and unexpected, considering the historical infrequency of wildfire occurrence, and poor adaptability of plants to fire in warm desert plant communities (Abella 2009; Abella et al. 2009). Because flower production requires substantial allocation of carbon, nutrient, and water resources, floral production in resource-poor environments, such as deserts (Hadley and Szarek 1981), may be closely linked to increased resource availability (Beatley 1974).

Plants that survive wildfires may produce more flowers relative to unburned areas, due to shifts in environmental conditions, such as soil hydrology and nutrient content (Webb et al. 2009). Increased water and nutrient relations and growth have been reported for desert shrubs surviving in fire disturbed areas even six years post-fire (Horn et al. in review). Immediately following wildfire, nitrogen stored in plant tissues are returned to the soil, strongly altering soil nutrient status (Esque et al. 2010). Increased foliar nitrogen has been reported for desert shrubs

surviving in fire disturbed areas (Horn et al. in review), however, soil nutrient pulses associated with such disturbances can dissipate within 1-2 years (Esque et al. 2010). This suggests that altered soil nutrient status, directly resulting from wildfire disturbances, may not be the primary mechanism driving increased flower production in burned areas 7- 9 years post-fire.

Competition release, resulting from shrub density reductions following wildfires, could reduce soil resource competition, and link increases in soil water and nutrients (Horn et al. in review) to increases in shrub floral production in burned landscapes (Brisson and Reynolds 1994; Holzapfel and Mahall 1999). Removal of neighboring vegetation increases plant water relations, and the death of nearby plants may allow surviving roots to extend into areas of former competitors (Fonteyn and Mahall 1981). Drastic wildfire reductions in shrub density (Table 1.5), coupled with the slow regeneration of native desert plant communities (Webb et al. 2009), suggests that competitive release may be the principal driver of fire effects on plant reproduction across burned landscapes.

Recent work comparing functional responses of desert perennial shrub species in burned and unburned areas reported positive physiological responses of plants surviving in areas disturbed by wildfire (Horn et al. in review). Although the exact mechanism(s) are poorly understood, enhanced nutrient and water acquisition by shrubs surviving in burned desert landscapes suggests that a link exists between fires, plant functional responses, and enhanced sexual reproductive effort.

4.2 Resilience of pollination services to fire

Successful fruit and seed production for wind, generalist, and specialist pollinated plants surviving in burned areas, suggests that fire does not affect plant sexual reproduction based on the specificity of plant-pollinator relationships in this desert ecosystem. Two large reviews evaluating plant sexual reproduction in response to habitat disturbance in general, report plant reproductive success to be considerably negatively affected for both generalist and specialist pollinated plants (Aizen et al. 2002; Aguilar et al. 2006). Data provided here, indicating the neutral to positive effect of fire disturbance on both generalist and specialist pollinated plants, may contrast expectations from the literature for several key reasons. (1) The vast majority of studies evaluating disturbance effects on plant pollination characterize responses from a single plant species, in a single flowering season (Aguilar et al. 2006). Additionally, the criteria for selecting study species may favor plants that are rare or threatened, suggesting that disturbance effects on plant pollination may actually be less severe than reported in the literature (Aguilar et al. 2006). (2) Fire disturbances are generally unique from other disturbance types, in that plants can be positively affected by fire (Kerstyn and Stiling 1999). Through reductions in competition, resource pulses, increased reproductive vigor (Brewer and Platt 1994) and reduced pathogen loads (Waldrop et al 1992; Kerstyn and Stiling 1999), fire can differentially affect plant reproduction across species and habitat types.

Differences in fruit and seed:ovule ratios between wind, generalist, and specialist pollinated plants in burned and unburned areas, suggests there are inherent trade-offs between pollination strategies and the efficiency of ovule fertilization associated with them. Fire had no effect on fruit and seed:ovule ratios for wind pollinated plants, however, wind pollination seed:ovule ratios were greatly reduced compared to generalist and specialist pollinated plants (Fig. 1.2). While wind pollinated plants are not at risk of losing pollination services due to the

loss of pollinators, seed production can be variable due to the high risk of wasting pollen during transport (Wilcock and Neiland 2002). Fire increased generalist plant fruit production in burned edge areas (Fig. 1.2), and only reduced seed:ovule ratios by 3% (Fig. 1.2), resulting in a significant increase in the number of seeds produced per shrub in burned edge areas. Resilience is expected in generalist plant-pollinator networks where the overall number of strong dependencies is low (Bascompte et al. 2006), and the utilization of many pollinating species may have buffered plant-pollinator relationships, maximizing pollination (Ashworth et al. 2004). Fire had no effect on specialist plant fruit production in burned edge areas (Fig. 1.2), and increased seed:ovule ratios by only 1% (Fig. 1.2), suggesting that specialized pollination services are consistent across burned and unburned desert landscapes. The high group seed:ovule ratios for specialist pollinated plants in unburned and burned edge areas (~65%) were heavily influenced by high *Yucca* seed:ovule ratios, which fire reduced by only 5% in burned edge areas (Table 1.2). While the loss of specialist pollinators can have the most catastrophic impact on plant reproductive success, specialist pollinators typically deliver high quality conspecific pollen (Ashman et al. 2004). Therefore, *Yucca* pollination success in burned areas may be attributed to yucca moth efficiency required to secure resources for developing moth larvae (Powell 1992). Reduced generalist seed:ovule ratios (~50%), relative to specialist pollinated plants (~65%), demonstrates the disadvantage of utilizing generalist pollinators, which can deliver pollen that is often tainted with incompatible pollen, blocking stamens and reducing seed:ovule ratios (Brown and Mitchell 2001).

Ultimately, fire effects on plant-pollinator interactions will depend largely on the resilience of networks to distributional mismatches that could result in the loss of pollination services to surviving or regenerating vegetation. In this study, isolation had no effect on

pollination services, measured as fruit set, across expansive burned landscapes (Fig. 1.2, Table 1.2). Successful fruit production in burned isolated, and burned edge locations for generalist and specialist pollinated plants, may be attributed to the efficiency and survivability of pollinators associated with desert pollination networks. Solitary bees compose the most diverse, abundant, and dominant pollinator group in arid and semi-arid regions (Michener 2000). The vast majority of desert solitary bee fauna nest underground and are largely expected to survive the immediate effects of wildfire (Cane and Neff 2011). The same may be true for yucca moths, which also “nest” underground in cocoons while in diapause (Pellmyr 2003). Considering the relatively limited foraging ranges of bees and yucca moths, successful fruit set in isolated burned areas (Fig. 1.2), suggests that pollinators are residing deep within burned landscapes, and are most likely not traveling 1.5-2km into these areas from adjacent unburned habitat, even though bees can fly great distances if necessary (Kunin 1993; Gathmann and Tschardt 2002; Marr et al. 2000). Fire may also sustain pollination success by generating nesting locations for pollinators in disturbed sites, indirectly improving floral rewards and overall plant attractiveness to pollinators (see section 4.1), and facilitating quality outcrossing by forcing pollinators to move greater distances between conspecific plants (Potts et al. 2003, 2005; Caruso et al. 2005; Dick 2008).

4.3 Yearly variation in flower, fruit, and seed:ovule ratios

Across years the magnitude of flower, fruit, and seed production fluctuated greatly between species and within some conspecific burn comparisons (Table 1.4). Generally, the largest proportions of flowers were produced in 2013 (Table 1.2), and increases compared to 2012 flower values, were significant for all species in burned edge, but not unburned areas (Table 1.4). Annual shifts in floral production may have resulted from differences in

precipitation leading up to, and during spring flowering and reproductive seasons (Beatley 1974). The minimum precipitation requirement (>25mm; Beatley 1974) to facilitate spring flowering in shrub species was met each study year, however, the timing and magnitude of precipitation events varied drastically within years (mesowest.utah.edu). In 2013, total March and April precipitation was 1.5 times greater than 2012, and nearly 3.5 times greater than in 2014 (mesowest.utah.edu). This late spring surge in precipitation may explain why flower production was so high in 2013 (Beatley 1974).

Consistent increases of flower production, associated with increased spring precipitation, in burned edge areas from 2012 to 2013 (Table 1.4), suggests that reproduction may be less water limited in areas disturbed by wildfire. Shrubs surviving in burned areas are generally less stressed for water than plants in unburned areas (Horn et al. in review), which may enable more water to be allocated to the synthesis and maintenance of reproductive structures.

Fluctuation in fruit and seed:ovule ratios did not appear to follow precipitation trends as closely as flower production throughout this study. Overall, fruit production was greatest in 2013, however, annual fluctuation in fruit set for individual species both increased and decreased in unburned and burned edge areas during our three year study period (Table 1.4). Shifts in annual reproductive success may be influenced by a variety of ecological factors that affect successful fruit and seed production. The timing of flowering, competition for pollinators, seed predation, and pollen limitation that plants experience as a natural condition, all may influence annual fluctuations in reproductive success, independent of fire effects, (Pettersson 1991; English-Loeb and Karban 1992; Dudash 1993; Burd 1994; Brody 1997). Further research

utilizing long-term (many years) patterns of plant sexual reproduction may provide a better understanding of annual reproductive response variation in desert landscapes.

4.4 Landscape changes in shrub flower and fruit production

Despite increased flower, fruit, and seed production per plant in burned areas (Table 1.2), unburned landscapes produced a greater total number of flowers, fruits, and seeds per unit ground area (Table 1.5). Shifts in total reproductive output across burned and unburned desert landscapes appear to be strongly linked with changes in plant density resulting from wildfire, as evidenced by flower and fruit reductions ranging from 30%-98% for species in burned edge locations, with the exception of *Encelia* flower production, and decreases in flower and fruit production ranging from 57%-100% in isolated burned areas, with the exception of *Thamnosma* fruit production (Table 1.5). Contrasting fire effects between landscape and individual plant comparisons emphasize the importance of scale considerations when evaluating disturbance effects on plant communities. Successful, and often increased flower, fruit, and seed production at the individual shrub level may partially compensate for reductions in landscape reproductive output, even though total seed production across burned landscapes is quite limited compared to unburned areas. Ultimately, the ability of individual plants to potentially offset landscape level reductions in flower, fruit, and seed production, will depend on the survivability of pollinating fauna, and the maintenance of pollination services across fire disturbed landscapes. Successful fruit and seed production of generalist and specialist pollinated plants in burned edge, and isolated burned areas suggests that pollinating species reside in, and are foraging across burned landscapes. Bottom-up effects, such as food availability, are critical for pollinator populations (Steffan-Dewenter and Schiele 2008), and increased food availability from generalist and

specialist pollinated plants surviving in burned areas may be able to compensate for potential diet reductions that pollinators may experience while foraging across burned landscapes.

Conclusions

The occurrence of wildfires will likely intensify as climate changes prolong growing seasons and increase temperature and drought events (Westerling et al. 2006). Additionally, exotic annual plant invasions increase the size and frequency of wildfires in many regions around the world (D'Antonio and Vitousek 1992). These changes together make the persistence of plant populations increasingly more dependent on the ability of pollinators to move across expanding fragmented landscapes (Amarasekare 2004). Fire disturbance can exhibit positive bottom-up effects on plant sexual reproduction through reductions in competition, resource pulses, and increased reproductive vigor that may compensate and regulate pollinator populations (Brewer and Platt 1994; Kerstyn and Stiling 1999; Steffan-Dewenter and Schiele 2008). Sexual reproduction provides an independent dispersal phase, increased genetic diversity opportunities, and the potential for populations to adapt to changing environmental conditions (Wilcock and Neiland 2002). Results on the effects of fire disturbance and isolation on plant reproduction suggest that fire increases, or has no effect on flower, fruit and seed production for wind, generalist, and specialist pollinated plant species. Pollination services are robust across desert landscapes, and are not affected by isolation from intact shrub communities. Such resilience, resulting in successful sexual reproduction, will be critical to the long-term sustainability of plant populations, and should continue as long as plant-pollinator interactions can overcome temporal or distributional mismatches that result in the loss of pollination services.

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Chapter 1: Tables

Table 1.1 Floral characters, reproduction system, and flower visitors of study species.

Plant species	Family	Sex of fl./plant	Breeding system	Specialization	Visitors
<i>Ambrosia dumosa</i>	<i>Asteraceae</i>	perfect	SI	W	n/a
<i>Coleogyne ramosissima</i>	<i>Rosaceae</i>	perfect	SI	W	n/a
<i>Larrea tridentata</i>	<i>Zygophyllaceae</i>	perfect	SC(limited)	G	bees
<i>Encelia farinosa</i>	<i>Asteraceae</i>	perfect	SI	G	bees, butterflies and moths
<i>Thamnosma montana</i>	<i>Rutaceae</i>	perfect		G	butterflies, bees
<i>Krameria grayi</i>	<i>Krameriaceae</i>	perfect	SI	S	bees, genus <i>Centris</i> (subg. <i>Paracentris</i>)
<i>Yucca brevifolia</i>	<i>Agavaceae</i>	perfect		S	Yucca moths

SI = self-incompatible, SC = self-compatible; W = wind pollinated, G = pollination generalist, S = pollination specialist

Table 1.2 Statistical summaries of glmmADMB mixed-effects linear models evaluating flower, fruit, and seed:ovule ratios in unburned and burned edge areas.

Flower Counts					
		$\bar{x} \pm SE (n)$		Z	Pr(> z)
		Unburned	Burned		
WIND					
	overall	485±94 (83)	1296±259 (50)	-3.21	0.001**
	2012 Ambrosia	384±156 (19)	1636±411 (13)	-2.01	0.044*
	2013 Ambrosia	1176±337 (18)	2438±665 (15)	-1.82	0.068
	2014 Ambrosia	90±35 (21)	249±127 (11)	-0.6	0.55
	2013 Coleogyne	394±88 (25)	383±117 (11)	-1.94	0.053
GENERALIST					
	overall	301±50 (158)	764±103 (158)	18.59	<0.001***
	2012 Larrea	187±44 (23)	712±127 (23)	-3.54	0.00047***
	2013 Larrea	568±220 (27)	1173±356 (23)	-2.46	0.014*
	2014 Larrea	677±146 (26)	2398±444 (22)	-3.37	0.00074***
	2012 Encelia	11±5 (13)	25±8 (20)	-1.17	0.24
	2013 Encelia	60±16 (23)	75±18 (25)	-0.82	0.41
	2014 Encelia	35±10 (21)	43±12 (21)	-0.04	0.97
	2013 Thamnosma	325±75 (25)	890±104 (24)	-4.78	1.8e-06***
SPECIALIST					
	overall	365±62 (75)	444±83 (50)	-1.85	0.06
	2013 Krameria	226±79 (25)	82±67 (13)	0.42	0.67
	2014 Krameria	6±2.49 (25)	6±2.79 (15)	-0.14	0.89
	2013 Yucca	862±111 (25)	959±114 (22)	-0.58	0.56
Fruit Counts					

	$\bar{x} \pm SE (n)$		Z	Pr(> z)
	Unburned	Burned		
WIND				
overall	202±49 (83)	188±61 (50)	0.24	0.81
2012 Ambrosia	8±6 (19)	80±20 (13)	-7.04	1.9e-12***
2013 Ambrosia	56±15 (18)	72±24 (15)	-1.17	0.24
2014 Ambrosia	1±0.5 (21)	5±3 (11)	-0.97	0.3303
2013 Coleogyne	622±127 (25)	655±233 (11)	-0.67	0.5
GENERALIST				
overall	281±43 (183)	736±88 (182)	16.24	<1e-04***
2012 Larrea	483±137 (23)	2278±366 (23)	-4.87	1.1e-06***
2013 Larrea	521±160 (27)	601±195 (23)	-0.32	0.75
2014 Larrea	456±180 (26)	1323±343 (22)	-1.65	0.098
2012 Encelia	16±7 (13)	32±13 (20)	-1.3	0.19
2013 Encelia	89±54 (23)	9±6 (25)	2.83	0.0047**
2014 Encelia	9±3 (21)	22±13 (21)	0.13	0.899
2013 Thamnosma	405±87 (25)	1197±117 (24)	-4.2	2.6e-05***
2014 Thamnosma	72±19 (25)	356±65 (24)	-4.2	2.6e-05***
SPECIALIST				
overall	65±13 (95)	68±9 (66)	-0.19	0.85
2012 Krameria	164±49 (20)	110±28 (16)	0.01	0.99
2013 Krameria	18±10 (25)	23±23 (13)	-0.13	0.9
2014 Krameria	4±2.2 (25)	1.06±1 (15)	-0.23	0.82
2013 Yucca	92±14 (25)	110±15 (22)	-0.93	0.35
S/O Ratio				
	$\bar{x} \pm SE (n)$		Z	Pr(> z)

	Unburned	Burned		
WIND				
overall	0.0058±0.003 (510)	0.01±0.002 (3677)	-0.09	0.93
2012 Ambrosia	0.008±0.005 (380)	0.01±0.002 (3528)	-0.88	0.38
2013 Ambrosia	0±0 (130)	0±0 (149)	0	1
GENERALIST				
overall	0.53±0.005 (9265)	0.5±0.005 (8968)	8.53	<1e-04***
2012 Larrea	0.79±0.006 (4000)	0.73±0.007 (4000)	5.93	3e-09***
2013 Larrea	0.10±0.013 (1386)	0.36±0.014 (1187)	-2.32	0.02*
2012 Encelia	0.37±0.009 (3146)	0.3±0.008 (3168)	-1.11	0.26
2013 Encelia	0.21±0.01 (733)	0.29±0.02 (613)	-2.82	0.0048**
SPECIALIST				
overall	0.64±0.005 (6453)	0.65±0.007 (4007)	-11.05	<1e-05***
2012 Krameria	0.04±0.008 (611)	0.07±0.02 (130)	-1.35	0.18
2013 Krameria	0.06±0.02 (176)	0±0 (19)	0.04	0.96
2013 Yucca	0.72±0.006 (5666)	0.67±0.008 (3858)	5.17	2.4e-07***

Significance designated as *P < 0.05, **P < 0.01, ***P < 0.001.

Table 1.3 Statistical summaries of glmmADMB mixed-effects linear models evaluating flower and fruit counts in burned edges and isolated burned areas by species and year.

		Flower Counts		Z	Pr(> z)
		$\bar{x} \pm SE (n)$			
		Burned Edge	Isolated Burn		
WIND					
	overall	-	-	-	-
GENERALIST					
	overall	764±103 (115)	674±151 (117)	-0.7	0.48
	2013 Larrea	1173±356 (23)	484±166 (25)	-1.34	0.18
	2014 Larrea	2398±444 (22)	2145±590 (25)	-0.29	0.78
	2013 Encelia	75±18 (25)	37±12 (25)	-1.11	0.27
	2014 Encelia	43±12 (21)	11±4 (17)	-1.85	0.056
	2013 Thamnosma	890±104 (24)	482±142 (25)	-0.5	0.62
SPECIALIST					
	overall	959±114 (22)	1101±161 (24)	0.28	0.78
	2013 Yucca	959±114 (22)	1101±161 (24)	0.28	0.78

		Fruit Counts		Z	Pr(> z)
		$\bar{x} \pm SE (n)$			
		Burned Edge	Isolated Burn		
WIND					
	overall	-	-	-	-
GENERALIST					
	overall	736±88 (139)	529±86 (141)	-1.04	0.3
	2013 Larrea	601±195 (23)	188±90 (25)	-1.42	0.16
	2014 Larrea	1323±343 (22)	859±377 (25)	-0.39	0.69

2013 Encelia	9±6 (25)	7±4 (25)	-0.4	0.69
2014 Encelia	22±13 (21)	2±0.72 (17)	-0.88	0.379
2013 Thamnosma	1197±117 (24)	1454±151 (25)	1.24	0.21
2014 Thamnosma	356±65 (24)	495±69 (24)	1.5	0.13
SPECIALIST				
overall	110±15 (22)	122±20 (24)	0.6	0.55
2013 Yucca	110±15 (22)	122±20 (24)	0.6	0.55

Significance designated as *P < 0.05, **P < 0.01, ***P < 0.001.

Table 1.4 Percent change in flower, fruit, and seed:ovule ratios across years, within unburned and burned edge areas. UB-UB = comparison of unburned areas; B-B = comparison of burned edge areas.

Species/Year	Flower		Fruit		S/O	
	UB - UB	B - B	UB - UB	B - B	UB - UB	B - B
<i>Ambrosia</i>						
2012-2013	+206%	+49%***	+605%***	+873%***	-100%	-100%
2013-2014	-92%	-89%*	-98%	-92%		
<i>Larrea</i>						
2012-2013	+203%	+64%***	+7%	-73%	-87%***	-50%***
2013-2014	+19%	+104%	-12%	+120%		
<i>Encelia</i>						
2012-2013	+445%	+200%***	+456%*	-71%***	-43%***	-3%**
2013-2014	-41%	-42%	-89%	+144%		
<i>Krameria</i>						
2012-2013	-	-	-89%	-79%***	+50%	-100%
2013-2014	-97%	-92%***	-77%	-95%		

Significance designated as *P < 0.05, **P < 0.01, ***P < 0.001.

Table 1.5 Mean shrub density and percent cover, with associated standard error values for each study species, with estimated flower and fruit production per m² based on plant density changes in unburned, burned edge, and isolated burned locations.

Species	Density			Cover			Flower			Fruit		
	Unburn plants plot ⁻¹	Burn plants plot ⁻¹	Isolated Burn plants plot ⁻¹	Unburn cover (%)	Burn cover (%)	Isolated Burn cover (%)	Unburn flower/ m ²	Burn flower/ m ²	Isolated Burn flower/ m ²	Unburn fruit/ m ²	Burn fruit/ m ²	Isolated Burned fruit/ m ²
Ambrosia	4.9±0.48	1.36±0.38	0	4.8±4.1	1.3±4.1*	0	2.98	2.08	0	1.2	0.82	0
Coleogyne	12.8±0.33	0.31±0.27*	0	30±4.9	0.7±5.1*	0	55.61	1.41	0	87.79	2.41	0
Larrea	2.7±0.18	0.59±0.17*	0.08±0.13**	20±6	2.4±4.3*	0.3±3.4	8.36	2.08	1.67	8.41	2.06	0.66
Encelia	0.5±0.27	0.78±0.28	0.24±0.21	1±3.8	1.2±3.5	0.2±3	0.17	0.25	0.03	0.18	0.1	0.006
Thamnosma	3.15±0.27	0.42±0.15*	1.08±0.13**	5.3±3.7	0.6±2.2*	1.4±3.2 ⁺	8.03	2.13	3.43	5.91	1.86	7.01
Krameria	2.4±0.22	0.31±0.16*	0	4.7±3.4	0.3±2*	0	0.5	0.007	0	0.24	0.008	0
Yucca	1.55±0.22	0.14±0.18*	0.66±0.38 ⁺	6.4±5.4	1±6.1*	0.6±4	6.58	0.88	0.56	0.7	0.1	0.06

Significance designated as *P < 0.05 for comparisons with unburned control plots, and ⁺P<0.05 to indicated statistical significant

between burned edge and isolated burned area comparisons.

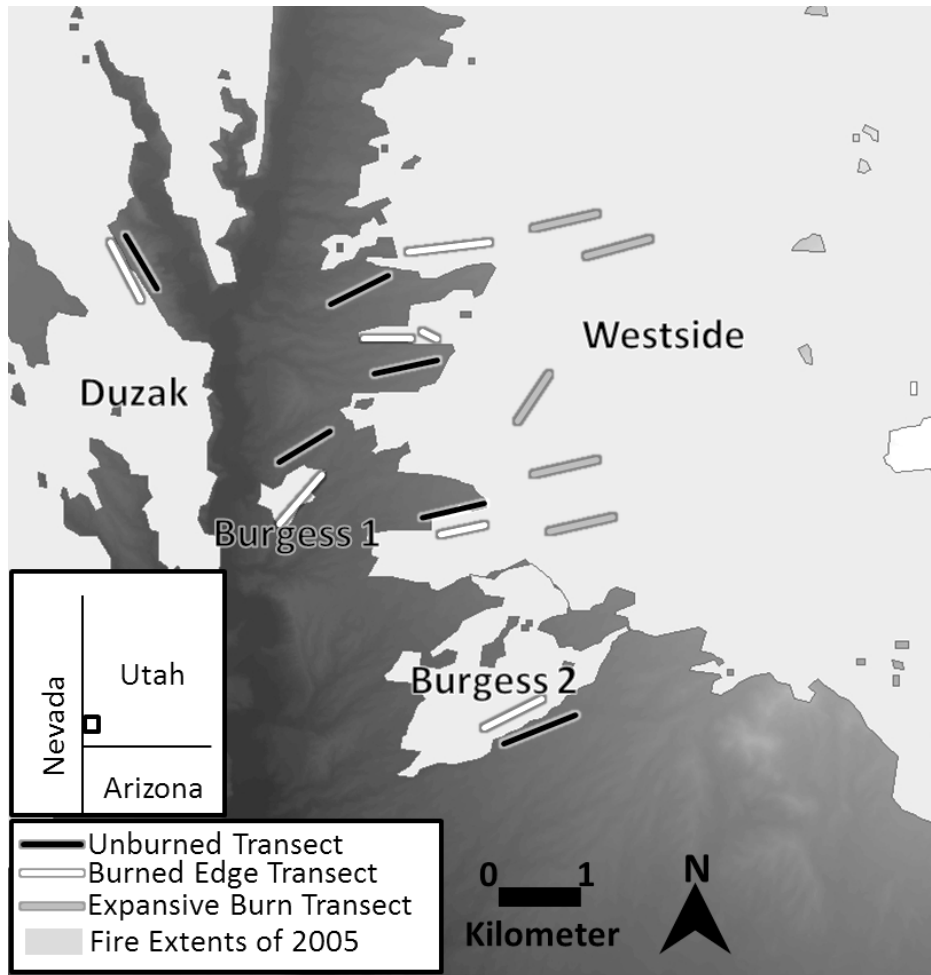


Fig. 1.1 Map of Beaver Dam Wash (N37.14, W114.03) study site. Transect lines in four independent burns (white) were paired with adjacent unburned transects (black). Isolated burn transect lines (light grey) were only established in the Westside fire. Study area denoted by black rectangle in southwest corner of Utah.

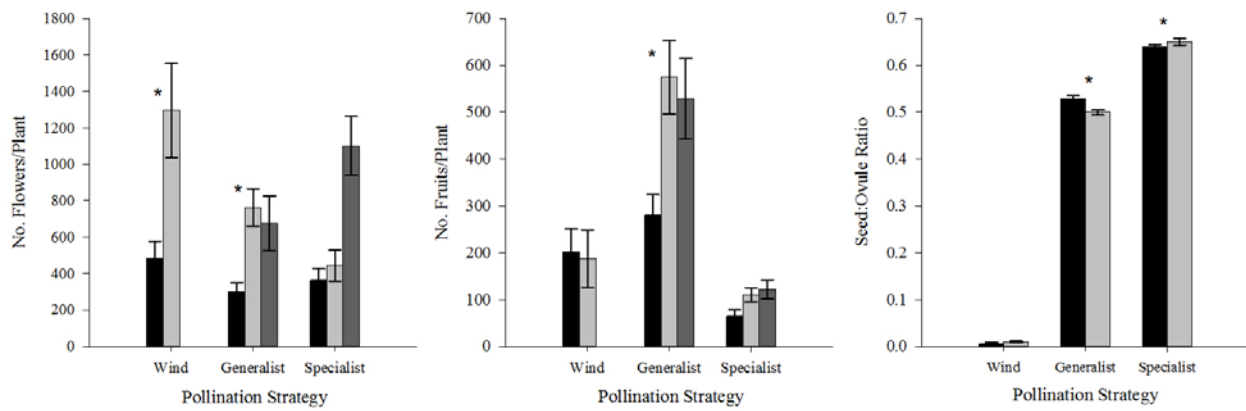


Fig. 1.2 Mean flower and fruit counts, and seed:ovule ratios for wind, generalist, and specialist pollinated plants in unburned (black bars), burned edges (light grey bars), and isolated burned (dark grey bars) areas \pm standard error values with ‘*’ indicating significance at $\alpha = 0.05$.

Chapter 2: Fire differentially affects reproductive output and flower herbivory in two dominant
Yucca (Agavaceae) species

Summary

Plants that depend on pollinator mutualisms may be at risk of experiencing reproductive failure if interactions with pollinators are hindered or lost. Currently the size, frequency and severity of wildfires and ungulate herbivory pressure are increasing at a global scale, including arid ecosystems that exhibit great sensitivity to disturbance. To understand how fire and ungulate herbivory affect reproductive success of specialist pollinated desert plants, we quantified the sexual reproductive effort, success, pollinator visitation, and proportion of floral consumption by ungulate herbivores for two yucca species (*Yucca baccata*, and *Yucca brevifolia*) in burned and unburned areas of the Mojave Desert. Wildfire and herbivore effects on plant reproduction were assessed comparing the proportion of flowering plants and floral herbivory, pollinator collections, and the number of flowers and fruits produced per plant in burned and unburned areas. These were assessed in the spring of 2013 and 2014 along paired burned-unburned transects and a grid of survey transects positioned across multiple independent fires that occurred in the Beaver Dam Wash of the Mojave Desert in 2005. Fire increased the proportion of *Y. baccata* flowering plants from 12% to 22% in burned areas, but had no effect on the number of flowers or fruits produced per plant for *Y. baccata* or *Y. brevifolia*. Fruit set and pollinator collection failed at all sampled *Y. baccata* individuals, while fire and herbivory had no effect on *Y. brevifolia* flower, fruit, and pollinator collection. Herbivores consumed 50% and 67% of floral stalks produced by *Y. baccata* in unburned and burned areas. Herbivores pose a clear threat to successful sexual reproduction in *Y. baccata*. Contrasting responses to ungulate herbivory between *Y. baccata* and *Y. brevifolia* may be due to morphological differences that position *Y.*

brevifolia reproductive tissues out of the reach of herbivores. Removal of ungulate herbivores during important flowering periods may still result in failed fruit and seed production if local pollinator reserves have been drastically reduced or lost.

1. Introduction

Pollinator mutualisms are fundamental to sexual reproduction in a majority of flowering plants species (Linder 1998; Renner 1998; Ackerman 2000; Pellmyr 2002). To attract pollinators, plant reproductive structures are conspicuous relative to other tissues (Fenster et al. 2004). Floral rewards consist of nectar, pollen, or edible parts, and advertisements include vibrant and specific floral colors and shapes with characteristic fragrances. However, plants are simultaneously subject to multiple selective pressures, and substantial resource allocation to attractive flower displays could be detrimental to plant fitness if displays entice harmful interactions, such as herbivory. Herbivore damage to plant foliar and reproductive tissues pose a threat to pollination services and can inhibit plant sexual reproduction (Hendrix 1988; Strauss et al. 2004). Direct consumption of flowers, fruits, and seeds can reduce reproductive success when structures are consumed or damaged to a degree that they fail to attract pollinators or sufficiently nurture potential propagules (Krupnick et al. 1999; Gómez and Zamora 2000; Mothershead and Marquis 2000).

Mutualistic and antagonistic interactions between plants and animals can be differentially affected by habitat disturbances that reduce plant population densities. Plant isolation can decrease sexual reproductive success directly through interference of plant-pollinator interactions (Kunin 1997; Groom 2001). Successful pollination is related both to the number of, and distance between flowers (Kunin 1997; Bosch and Waser 1999; Wailes and Agren 2004). Fewer plants

across a landscape reduces the amount of pollen available for successful outcrossing, and requires pollinators to travel greater distances between plants. In addition, increasing isolation can affect plant herbivory, intensifying or reducing consumption in disturbed areas (Groom 2001; Kolb 2008). The overall outcome of these interactions may be determined by the strength of the relationships between plants and their associated mutualists and antagonists.

Plant dependence on animal pollinators varies widely between species. Plants that depend on one or a few related taxa for pollination services may be at greater risk of experiencing reproductive failure when interactions with pollinators are hindered or lost (Bond 1994). Pollinators involved in these specialized plant-pollinator associations generally deliver higher quality pollen loads than floral generalist (i.e., plants pollinated by a wider taxonomic variety of species). Currently no empirical evidence suggests that specialist plants are more likely to experience Allee effects or risk of extinction resulting from habitat disturbances (Aizen et al. 2002; Ghazoul 2005). Lack of support may be due to an absence of symmetric plant-pollinator relationships (i.e., relationships defined by a specialist plant and specialist pollinator) that have been evaluated in nature (Ashworth et al. 2004 and references therein). Analysis of disturbance effects on pollinator visitation and plant reproductive success in highly specialized plant-pollinator relationships, such as those utilized by *Yucca* (*Agavaceae*) species and their associated yucca-moth pollinators (*Tegeticula* and *Parategeticula*) is currently lacking.

Human activities are increasing the size, frequency and severity of wildfires and ungulate herbivory pressure at a global scale (Weisburg and Bugmann 2003; Hebblewhite et al. 2005; Bowman et al. 2009), including arid ecosystems that exhibit great sensitivity to disturbance. In the Mojave, Great Basin and Sonoran Deserts the frequency and size of wildfires has surged in recent decades due to the invasion of exotic annual grasses (Schmid and Rogers 1988; Brooks et

al. 2004; Bukowski and Baker 2013). Grass invasions have been associated with livestock herbivory (D'Antonio and Vitousek 1992). Herbivory pressure in arid and semiarid regions of North America has increased with the introduction of livestock, significantly impacting plant communities through reductions in total vegetation biomass as well as grass and shrub cover (Jones 2000). Plant reproduction can be severely impacted by the direct consumption of reproductive tissues when livestock occupy desert ranges during plant flowering seasons (Kerley et al. 1993). While fire and ungulate herbivory independently threaten the resilience of native desert communities, the interactive effect of these disturbances on plant reproductive success in arid systems has not previously been evaluated (Brooks 2000; Jones 2000). Because herbivore foraging intensity can shift based on changes in plant density (Groom 2001; Kolb 2008), and wildfires reduce native vegetation (McLaughlin and Bowers 1982), it is possible that fire disturbances may indirectly affect the reproduction of surviving or regenerating vegetation in burned areas. It is unclear however, if changes in available forage will increase or relieve herbivore pressure on plants in burned areas. Herbivore effects on plant communities may be determined by a complex of variables such as plant palatability, nutritional value, and tolerance and animal population size and behavior (Augustine and McNaughton 1998). Overlapping increases in ungulate herbivory and wildfire provide an opportunity to understand how interacting disturbances influence pollination mutualisms and the reproductive success of plant species.

With the global increase of wildfires and their predicted expansion under future climate scenarios (Lenihan et al. 2003, IPCC 2007), coinciding with ungulate populations there is a critical need to better understand wildfire and herbivory effects on plant reproductive systems. Herein we characterize pollinator visitation, floral herbivory and plant reproductive success of

Yucca brevifolia and *Yucca baccata*, two species with highly specialized pollinator mutualisms, in adjacent burned and unburned habitats of the northeastern Mojave Desert to address the following questions: 1) Is there significant floral herbivory by ungulates in desert systems and is it modified by fire? 2) Does fire influence yucca moth visitation to *Yucca* flower panicles? 2) Do plant reproductive responses to fire and herbivory vary between two dominant yucca species with contrasting growth forms?

2. Methods

2.1 Study location

This study was carried out in the Beaver Dam Wash (BDW) in the Mojave Desert of southwestern Utah during the summer of 2013. The northeastern region of the Mojave Desert is characterized by low growing perennial shrubs (Cody 1986a, 1986b). The dominant flora consists of Blackbrush (*Coleogyne ramosissima*), creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), Joshua tree (*Yucca brevifolia*) and Datil Yucca (*Yucca baccata*). The landscape has experienced large-scale fires in recent years and invasive species including red-stem filaree (*Erodium cicutarium*) and the winter annual red brome (*Bromus rubens*) are ubiquitous across the landscape. Sampling transects were located along three individual fires that occurred in the summer of 2005: Westside (June, 27,059 ha), Burgess 1 (July, 60 ha), and Burgess 2 (July, 712 ha) (Utah Bureau of Land Management).

2.2 Study species

Yucca species vary in size from small rosettes to large, arborescent plants, all producing panicle inflorescences containing tens to hundreds of flowers pollinated by yucca moths. *Yucca*

baccata Torr. (Agavaceae), (hereafter referred to as ‘*Y. baccata*’) is a widespread native perennial shrub, distributed across American southwestern states and northern Mexico (Hasting et al. 1972). The leaves are densely clustered around the stem near the ground and consist of concave, rigid structures that support recurved fibers along the margins and end with a stiff spine at the apex. Flowers are produced in dense panicles found mostly among the leaves. Reproduction is possible through successful pollen transfer and the propagation of basal nodules and sprouts from rhizomes.

Yucca brevifolia Engelm. (hereafter referred to as ‘*Y. brevifolia*’) is an arborescent species that can reach heights greater than 5 m. Its range generally follows Mojave Desert boundaries from southwestern Utah into southern Nevada, western Arizona, and into southeastern California (Kearney and Peebles 1960; Munz 1974; Welsh et al. 1993). Tree size and growth form often vary with site and climate conditions (Maxwell 1971; Munz 1974; Hickman 1993). Flowers occur in dense, heavy panicles (Johnson 1970; Hickman 1993). Seed production is periodic or rare, and wet years are suggested as best for flowering and fruit production (Maxwell 1971; Kliemann 1979).

All species of *Yucca* (Agavaceae) are pollinated by moth species in the genera *Tegiticula* and *Parategiticula* (Proxidae), and the biology and activity patterns of the distinct *Y. baccata* and *Y. brevifolia* pollinator species are similar (Pellmyr 2003). After emerging from pupation near the base of yucca plants, female moths collect pollen, and fly to another panicle. Eggs are oviposited into the ovary of a new flower, which is then followed by deposition of pollen on the stigmatic surface. Maturation of the flower into fruit is vital for the survival of the developing larvae, which feed exclusively on yucca seeds. Not all seeds are consumed, allowing both the *Yucca* and yucca moth to reproduce (Powell 1992).

2.3 Reproduction and herbivory survey

Two sample methods were used to characterize the number of flowers, fruits, and floral panicles produced and consumed for each species. For *Y. brevifolia* flower and fruit counts were collected along five 1 km transect pairs positioned along adjacent burned per unburned boundaries (Fig. 2.1). Transect pairs were positioned 200m on either side of a burn boundary. We selected a *Y. brevifolia* individual in closest proximity to each 200m increment marker along all transects (5 plants per transect). Individual plants were marked with a specific rounded aluminum numerical identification tag and a GPS waypoint was taken so we could repeatedly monitor the same individuals. To limit selection bias, all individuals were chosen before any flowering had occurred. *Y. brevifolia* flower and fruit counts were conducted from March-June of 2013. Flower panicles for each plant were counted during the peak flowering period. Average flower per panicle counts were determined by removing 2 panicles from each of 5 individual plants (outside of the study) in both burned and unburned areas and counting the number of flowers contained therein. Total flower counts per plant were then calculated by multiplying the total number of panicles by the average number of flowers per panicle as calculated above. Fruit counts were completed 2-3 weeks after flowering had ceased; due to their large distinct size, all fruits were counted.

Observation suggested the occurrence of floral herbivory in *Y. Brevifolia*, but only rarely, making it necessary to extend our survey beyond the paired transects to get enough observations to accurately determine herbivory frequency. We set up an additional 12 transects in unburned and burned locations spread 2.5 km apart to get broad survey coverage across the landscape.

To assess flowering, fruit set and browsing proportion for *Y. baccata*, a grid of 29 survey transects was established across the Beaver Dam Wash (16 in burned landscapes and 14 in unburned areas). Site selection was standardized by distance, each spaced approximately 2.5 kilometers from each other to get even coverage across the Beaver Dam Wash. The survey was conducted the first two weeks of June 2013 after cattle were removed from the landscape (June 1, 2013). At each site plants were evaluated to determine whether they had flowered and if those that had flowered had been damaged or removed. Flower per panicle counts for *Y. baccata* were determined by obtaining flower counts on 30 panicles to generate an average flower count per panicle for the species. To experimentally control for ungulate browsing we placed wire fence approximately 2m tall, around 10 *Y. baccata* (5 in burned areas, 5 in unburned locations) at various locations across our sampling grid that allowed access to small, but not large, mammals .

2.4 Yucca moth trapping

Sticky traps were used to assess pollinator visitation to flowers of both *Yucca* species. Traps were installed on ten *Y. baccata* plants within the exclosures described above. *Y. baccata* traps were created by cutting an office file folder into rectangles (approximately 3x20cm). A single rectangular “tag” was then attached to a panicle stalk at half the panicle height using a zip tie. Tangle trap natural insect trapping adhesive (BioQuip products) was applied to trap surfaces to ensure any insect that landed on the trap, or that brushed the surface while moving from flower to flower on the panicle would be trapped. *Y. brevifolia* traps were similar to *Y. baccata* traps, but were bowed and fastened together at the ends to form a cylinder which could then be placed around a single panicle. Tangle trap was applied to the inside of the cylinder. Twenty-five of the initial 58 traps were destroyed or lost due to high winds and storm weather, resulting in 33 total traps (13 unburned, 20 burned). Traps were positioned on panicles containing open,

sexually receptive flowers for two week trapping periods. *Y. brevifolia* moth trapping occurred from 25 March – 5 April of 2013, and *Y. baccata* trapping was completed from 15 April – 26 April 2014.

2.5 Statistical analysis

Mixed-effects linear models were used to examine fire and herbivore effects on flower, fruit and moth abundance proportions using either Automatic Differentiation Model Builder (glmmADMB) or lme4: Linear mixed-effects models using Eigen and S4. Automatic Differentiation Model Builder fits mixed effects models to count data using Poisson or negative binomial response distributions (Skaug et al. 2011), and lme4 was used to analyze normally distributed, equal variance data sets (Bates et al. 2014). In our mixed-effects models burn type and herbivory proportions were specified as fixed effects; sample site was specified as a random effect to account for uncontrolled landscape variation. The proportion of flowering plants and flower set per plant for *Y. baccata*, and herbivory proportions for *Y. brevifolia* were modeled using the lme4 package. Moth visitations per panicle for both yucca species were square root transformed to meet assumptions of normality and therefore modeled using the lme4 package. Flower and fruit set per plant for *Y. brevifolia* were modeled with a negative binomial distribution using the glmmADMB package, which fits biological count data well, and provides greater flexibility in evaluating a variety of patterns in animal or plant distributions (White and Bennetts 1996). Herbivory proportions of *Y. baccata* were evaluated using a binomial distribution in glmmADMB due to the binary response (eaten = 1, not eaten = 0) that results from the production of only a single panicle of flowers per plant. Assumptions of normality and homoscedasticity for each model, were inspected using comparisons of variance and residual plots (e.g. histogram, scatterplot, and qqnorm of residuals), and the best fit model distributions

were determined based on log-likelihood values. All calculations, models, assumption analyses and determinations of statistical significance were performed using program R software language and environment for statistical computing (R Development Core Team 2008).

3. Results

3.1 Fire effect on *Yucca* reproductive effort and success

Fire nearly doubled the proportion of *Y. baccata* plants that produced flowers in burned compared to unburned areas (12% vs. 22%) ($p < 0.001$; Fig. 2.2, Table 2.2). However, the proportion of *Y. baccata* individuals that produced fruits was zero for both burned and unburned areas, despite the significant increase in floral production within burned areas. Even panicles protected by ungulate exclosures failed to set fruit in burned or unburned areas, resulting in complete reproductive failure for all *Y. baccata* plants surveyed.

Fire had no effect on the number of flowers produced per plant for *Y. baccata* or *Y. brevifolia* (Fig. 2.3, Tables 2.1 and 2.2). Although flowering *Y. baccata* individuals failed to produce fruits, *Y. brevifolia* fruit production was successful in burned and unburned areas and fire had no effect on the number of fruits produced per plant (Fig. 2.3, Table 2.1).

3.2 Flower herbivory

Herbivores effected plant reproduction very differently for each *Yucca* species. Half of all *Y. baccata* flowers produced in unburned areas were significantly damaged or eaten, and floral consumption increased 17% in burned areas (50% vs. 67%) ($p < 0.001$; Fig. 2.4, Table 2.1). Herbivory of *Y. brevifolia* panicles was rare and did not differ between burned and unburned areas (Fig. 2.4, Table 2.2).

3.3 Fire effect on yucca moth visitation

Moth visits varied strongly between *Yucca* species and were not affected by fire. *Y. baccata* traps failed to indicate any pollinator visitation, with counts of zero for both burned and unburned areas (Fig. 2.5). *Y. brevifolia* traps indicated that moth visits in burned and unburned areas were not significantly different (Fig. 2.5, Table 2.2).

4. Discussion

4.1 Fire effects on *Yucca* reproductive effort

Fire enhanced *Yucca* reproductive effort by increasing the proportion of *Y. baccata* individuals that produced flowers in 2013 from 12% in unburned areas to 22% in burned landscapes (Fig. 2.2). Flower production requires substantial allocation of carbon, nutrient, and water resources, and may therefore be considered a high-risk investment (Bloom et al. 1985). Due to these high costs plants in resource-poor environments, such as deserts (Hadley and Szarek 1981), may not initiate flower production until specific resource thresholds have been met (Beatley 1974). The high proportion of flowering *Y. baccata* individuals in burned areas may be due to positive responses of surviving or regenerating plants in these areas to post-fire burn conditions. Plants surviving in burned landscapes experience shifts in environmental conditions (Webb et al. 2009), and reductions in soil resource competition due to decreased plant density following wildfires (Brisson and Reynolds 1994; Holzapfel and Mahall 1999). Increased carbon metabolism, nutrient acquisition and improved water relations have been recorded for surviving vegetation in post-wildfire desert landscapes (Horn et al. in review).

4.2 Fire and herbivory effects on *Yucca* reproductive structures

Herbivores consumed substantial proportions of *Y. baccata* panicles in both burned and unburned areas of the Beaver Dam Wash in 2013 (Fig. 2.4). In burned areas 67% of floral stalks produced by *Y. baccata* individuals were eaten by ungulate herbivores. Much higher proportions have been observed for *Y. elata* populations in southern New Mexico, reporting 98% of floral stalk consumption at sites where livestock were allowed access to plants during the flowering season (Kerley et al. 1993). Cattle have been reported to fight over and even stand on their hind legs to reach *Y. elata* flowers, and both floral and foliar tissue have composed up to 70% of livestock diets during dry winter and spring seasons (Herbel and Nelson 1966). Despite high levels of *Y. elata* floral consumption, Kerley et al. (1993) also reported that caudices produced above 1.7m in height suffered no flower grazing by livestock. This apparent “height escape” may explain why floral herbivory varied so drastically between *Y. baccata* and *Y. brevifolia* individuals (Fig. 2.4).

Variation in floral herbivory between *Y. baccata* and *Y. brevifolia* is most likely the result of different growth form strategies. Mature *Y. brevifolia* heights can range from 6-9m, and the earliest flowers are not usually produced until plants have reached 2.5-3m in height (McKelvey 1935). Browsing for many ungulates is limited to heights <2m, suggesting that low herbivory proportions for *Y. brevifolia* compared to *Y. baccata* might be explained by taller branch heights, which separate the majority of flowers produced by *Y. brevifolia* from the reach of herbivores (Kay 1990; Kerley et al. 1993; Zamora et al. 2001). It is possible that the towering heights reached by *Y. brevifolia* are the vestige of a growth escape strategy from now extinct megaherbivores. Analysis of the Shasta ground sloth (*Nothrotheriops shastensis* Sinclair) dung suggests that *Y. brevifolia* was a primary component of the megaherbivore’s diet (Harrington 1933; Lauder milk and Munz 1934). Understanding what other selective advantage(s) a desert

succulent gains by reaching such unusual heights is perplexing at best. The structural resource requirements and consequential lowering of xylem water potential associated with greater height represent a costly investment, especially in an ecosystem characterized by low water and soil resource availability and little to no light limitation (Hadley and Szarek 1981). It is possible that increased height may facilitate water storage in the stem or the avoidance of light limitation, high surface temperatures, or wildfires however, these benefits might well be accomplished with a lower average vertical growth than is currently reported for the species. Although further testing and analyses are required to better understand why *Y. brevifolia* grows much taller than other Mojave Desert shrubs and related *Yucca* species, the high positioning of flower panicles associated with taller individuals best explains the distinct patterns of herbivory observed between the study species.

4.3 Fire effects on *Yucca* reproductive success and yucca moth floral visitation

Contrasting proportions of fruit set for *Y. baccata* and *Y. brevifolia* emphasize the high potential risk often associated with plants that utilize specialized pollinators. Additionally, the differential responses observed in this study reiterate the importance of evaluating effects on both plants and their associated pollinators when predicting plant reproductive responses to habitat disturbances (Ashworth et al. 2004). *Y. brevifolia* individuals in burned areas had approximately the same proportion of fruits per plant and moths visits as plants in unburned areas, despite lower densities in post-fire landscapes (Horn et al. in review), which can result in lower reproductive success (Kunin 1997). The flight ability of yucca moths appears limited, with 80% of pollen transfers occurring within 8m of the source plant for *Y. filamentosa* (Agavaceae) (Marr et al. 2000), suggesting moths in burned areas were residents, not colonists, of such areas. Ground nesting solitary bees are largely expected to survive the immediate effects of fire (Cane

and Neff 2011), and the same may be true for yucca moths, which also “nest” underground in cocoons while in diapause (Pellmyr 2003), but further tests are required to determine moth survivability following desert wildfires.

The complete failure of *Y. baccata* fruit set and lack of moth visitation demonstrate the consequential impact that disrupted specialized plant-pollinator interactions can have on plant reproductive success. It is possible that fruits were produced and aborted, but selective fruit abortion in *Yuccas* is often the result of resource, not pollinator limitation (Udovic and Aker 1981; James et al. 1994). Fruits may also be aborted to mitigate seed consumption in pollinating seed-eating systems when the cost of lost seed outweighs the benefits of pollination (Pellmyr and Huth 1994; Shapiro and Addicott 2004), however, the absence of yucca moths from sticky traps, coupled with two years of failed fruit production, suggests *Y. baccata* panicles were not successfully pollinated (Fig. 2.3 and 2.5).

High levels of ungulate herbivory contributed to the reproductive failure of *Y. baccata* in both burned and unburned areas (Fig. 2.4). The lack of yucca moth pollinators most likely contributed to the failure of undamaged panicles to successfully set fruit in 2013 and 2014. When high proportions of flowers are consumed by herbivores, yucca moth reproduction may fail, depleting the abundance of future pollinators. Low pollinator abundance coupled with the limited foraging ranges associated with yucca moths may explain why undamaged *Y. baccata* flowers failed to be pollinated. If ungulate herbivores were removed to allow flowering to occur unhindered, successful fruit set may still not occur if local reserves of diapausing larvae have been drastically reduced or lost. Such vulnerability can result from specialization characterized by a high degree of mutual dependence when a component species on either the plant or pollinator side of a relationship is lost (Bond 1995; Kearns et al. 1998).

Management implications

Ecological disturbances affect plant-pollinator interactions in various ways (Kearns et al. 1998 and references therein). Evidence provided here indicate the danger that ungulate herbivores can be to plant seed production. Temporarily excluding large ungulates from *Yucca* populations during peak flowering periods may provide the necessary opportunity for disrupted plant-pollinator interactions to recover. Additionally, fire is considered a major threat to the maintenance of arid ecosystem processes and the conservation of native plants and animals in the Mojave Desert (Lovich and Bainbridge 1999). Although fire is not reported to affect plant reproductive success here, the occurrence of fire disturbance is most likely going to intensify, and the persistence of plant populations will therefore be more dependent on pollinators successfully transferring pollen across increasingly fragmented landscapes (Amarasekare 2004; Westerling et al. 2006).

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Chapter 2: Tables

Table 2.1 Z-values from glmmADMB linear mixed-effects models examining flower, fruit, and browsing proportions.

Source	$\bar{x} \pm SE (n)$		Z	Pr(> z)
	Unburned	Burned		
Y. brevifolia				
Flowers per plant	862±111(25)	959±114(22)	-0.58	0.56
Fruits per plant	92±14(25)	110±15(22)	-0.93	0.35
Y. baccata				
Floral Herbivory(%)	50±1.6(966)	67±1.0(2034)	-3.88	<0.001***

Significance designated as *P < 0.05, **P < 0.01, ***P < 0.001.

Table 2.2 LMER mixed-effects linear models examining the proportion of *Y. baccata* that flowered, the number of flowers per panicle for both *Y. baccata* and *Y. brevifolia*, and the numbers of moths collected per trap per two week trapping period for *Y. brevifolia* as a function of fire.

Source	$\bar{x} \pm SE (n)$		F	Pr(>F)
	Unburned	Burned		
<i>Y. baccata</i>				
Flowering Plants(%)	12±0.38(7735)	22±0.44(9051)	28.78	<0.001**
Flowers per Plant	43±9.53(10)	59±3.76(10)	2.67	0.17
<i>Y. brevifolia</i>				
Floral Herbivory(%)	1.2±0.1(966)	3.1±1.2(2036)	2.58	0.35
Moths per Panicle	8±1.58(13)	7±.96(20)	0.41	0.72

Significance designated as *P < 0.05, **P < 0.01, ***P < 0.001.

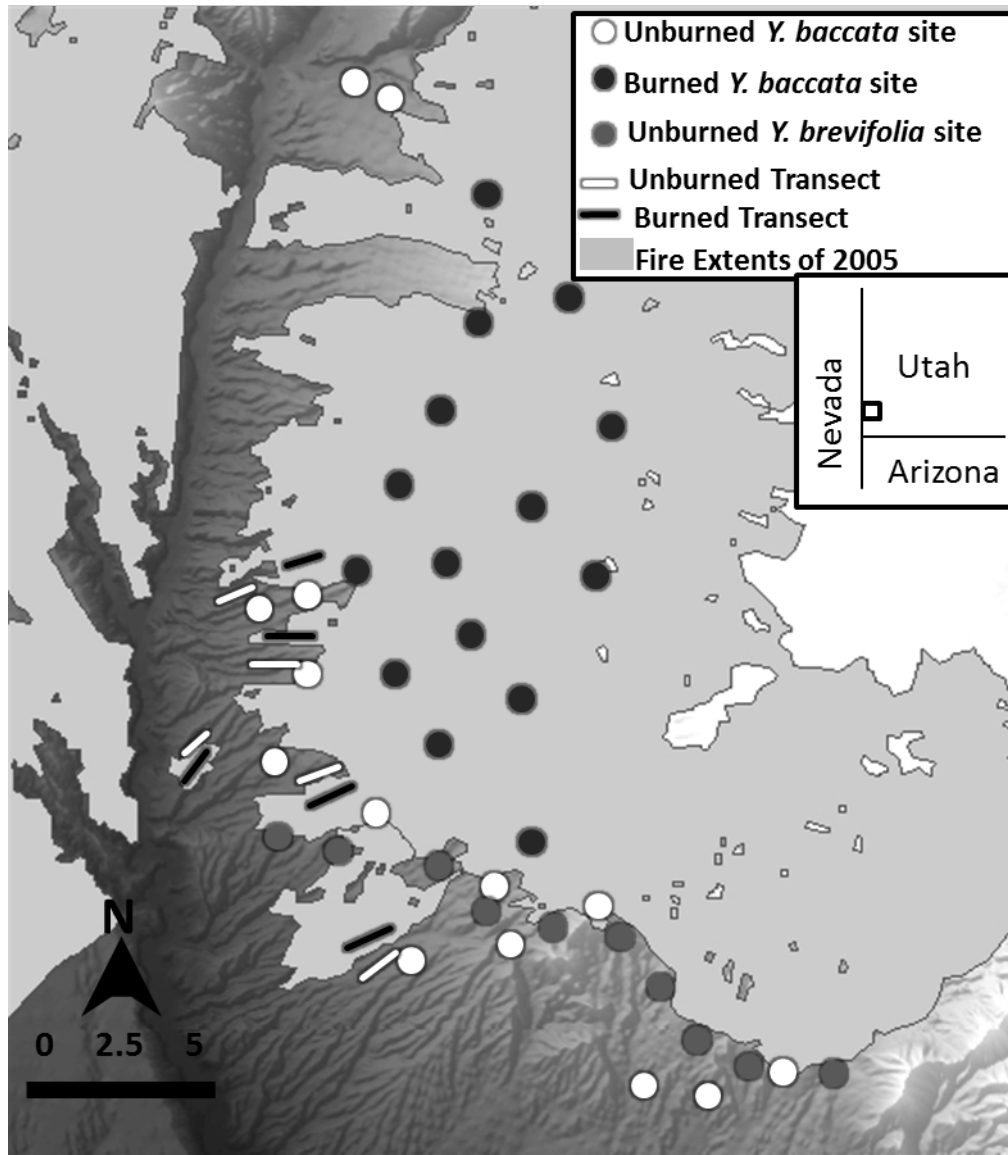


Fig. 2.1 Map of Beaver Dam Wash (n37.14, W114.03) study site. Transect lines in unburned areas (white) were paired with adjacent burned transect lines (black). *Y. baccata* browse and flower data collected in burned locations (black circles) and unburned locations (white circles). *Y. brevifolia* browse data collected in unburned areas (grey circles). Study area denoted by black rectangle in southwest corner of Utah.

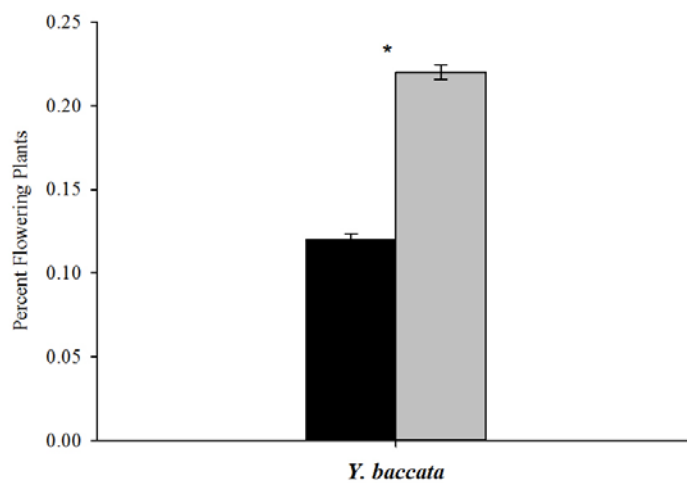


Fig. 2.2 The mean proportion (percent) of plants that flowered in unburned (black bars) and burned (grey bars) areas for *Y. baccata* and *Y. brevifolia* \pm standard error values.

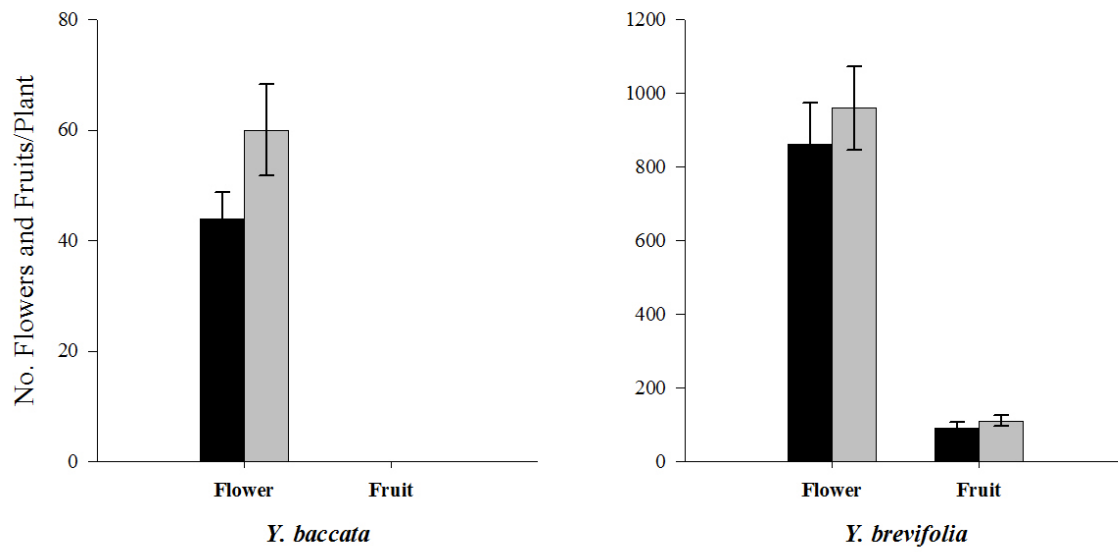


Fig. 2.3 The mean number of flowers and fruits produced per plant in unburned (black bars) and burned (grey bars) areas for *Y. baccata* and *Y. brevifolia* \pm standard error values.

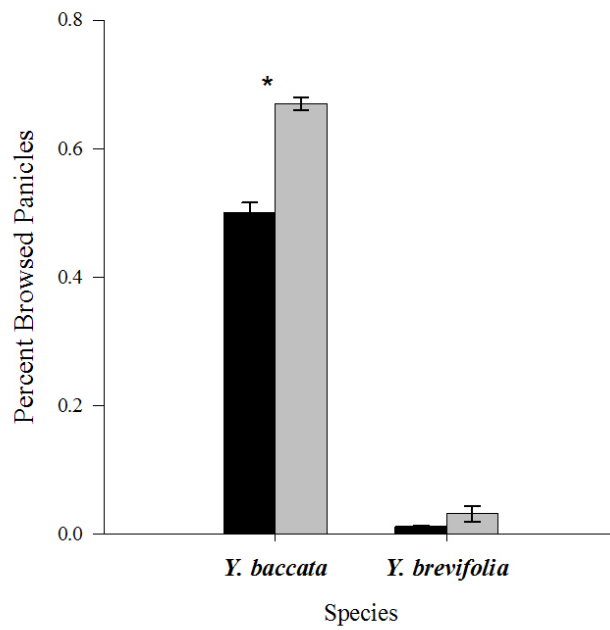


Fig. 2.4 The mean proportion (percent) of panicles that were severely damaged or completely consumed by large ungulate herbivory in unburned (black bars) and burned (grey bars) areas for *Y. baccata* and *Y. brevifolia* \pm standard error values.

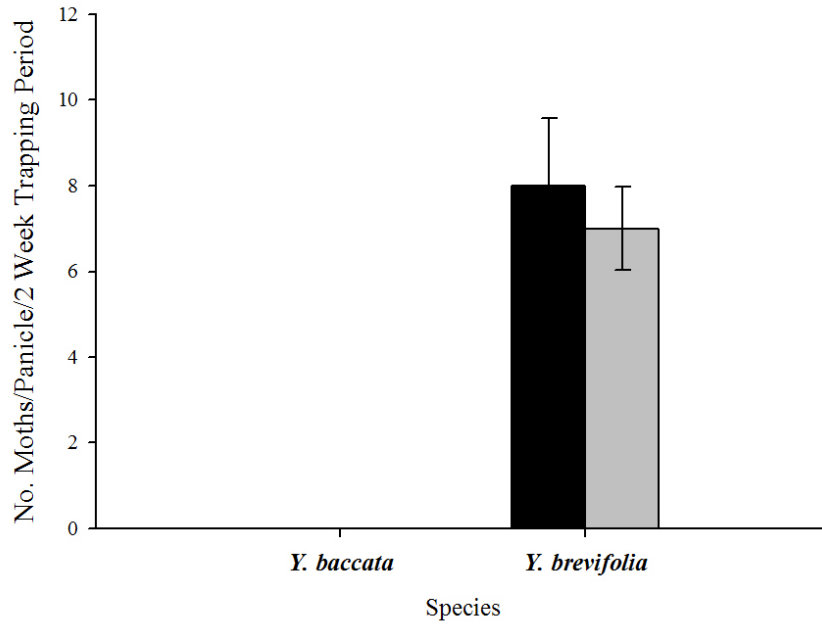


Fig. 2.5 The mean number of *Tegtacula* moths counted per trap (1 panicle) per two week trapping period in unburned (black bars) and burned (grey bars) areas for *Y. baccata* and *Y. brevifolia* \pm standard error values.