5-2013

Interspecific interactions between Penstemon palmeri and shrubs in the arid shrublands of the Spring Mountains, Nevada

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Recommended Citation

Poulos, Jesse M., "Interspecific interactions between Penstemon palmeri and shrubs in the arid shrublands of the Spring Mountains, Nevada" (2013). *All Graduate Theses and Dissertations*. 1966.
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INTERSPECIFIC INTERACTIONS BETWEEN *PENSTEMON PALMERI* AND SHRUBS IN THE ARID SHRUBLANDS OF THE SPRING MOUNTAINS, NEVADA

by

Jesse M. Poulos

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

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UTAH STATE UNIVERSITY
Logan, Utah

2013

ABSTRACT

Interspecific Interactions Between *Penstemon palmeri* and Shrubs in the Arid Shrublands of the Spring Mountains, Nevada

by

Jesse M. Poulos, Master of Science

Utah State University, 2013

Major Professor: Dr. Eugene W. Schupp
Department: Wildland Resources

A project involving shrub removal was undertaken by the United States Forest Service in the Spring Mountains National Recreation Area (SMNRA) to reduce accumulated woody fuels, which can pose risks to human communities. This research focuses on the interactions between shrubs and the perennial forb Palmer's penstemon (*Penstemon palmeri*), one of many nectar sources for the endemic Spring Mountains Acastus Checkerspot Butterfly (*Chlosyne acastus* ssp *robusta).* Initial observations revealed that *P. palmeri* ('penstemon') seemed to grow almost exclusively under shrubs. Such spatial associations are often indicative of a history of positive interactions between plants, and led to the research presented here. These studies investigate and discuss the interactions between this penstemon and shrubs in the arid shrublands of the SMNRA. Spatial patterns between populations of penstemon and shrubs were measured during November 2008-May 2011, and the consequences of shrub-association for individual penstemon emergence, survival, growth, and reproduction were documented (Chapter 2). The results suggest that although shrubs reduced penstemon emergence, they increased seedling survival (a seed-seedling conflict) resulting in a strong shift toward association between shrubs and penstemon over time. Further, while no differences in growth were detected between microhabitats, the results suggest that shrubs inhibited *P. palmeri* flowering but improved the successful maturation of fruits when flowering occurred. The mechanisms driving these patterns were elusive, but seed-sowing and seedling transplant experiments suggested that shrub soils, rather than their canopies, alter the nature of seed-seedling conflicts in a way that may promote seed-bank persistence in penstemon populations (Chapter 3). To provide a detailed description of the reproductive response of penstemon to shrubs, structural equation modeling was used to describe the importance of shrubs for penstemon seed production (Chapter 4). The results suggest that competition with shrubs reduced penstemon seed production, but that shrubs simultaneously facilitated penstemon water balance and altered the foraging behavior of its pollinators, indirectly increasing seed production. I conclude by discussing the importance of these studies, and studies of plant interactions in general, for helping land managers balance the objectives of fuel load reduction with protecting desirable species (Chapter 5).

(160 pages)

PUBLIC ABSTRACT

Interspecific Interactions Between *Penstemon palmeri* and Shrubs in the Arid Shrublands of the Spring Mountains, Nevada

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A project involving shrub removal was undertaken by the United States Forest Service in the Spring Mountains National Recreation Area (SMNRA) to reduce accumulated woody fuels, which can pose risks to human communities. The SMNRA is also home to a variety of species that occur within these fuel reduction boundaries and are protected under the Multiple Species Habitat Conservation Plan (MSHCP) of Clark County, Nevada. It is unknown how MSHCP covered species will respond to shrub removal. This research focuses on the interactions between shrubs and the herbaceous plant Palmer's penstemon (*Penstemon palmeri*), one of many nectar sources for the adults of MSHCP-covered Spring Mountains Acastus Checkerspot Butterfly (*Chlosyne acastus* ssp *robusta).* To understand the potential impact of shrub removal on *P. palmeri*, a series of observations and experiments were conducted. I begin by discussing plant interactions and the management concerns of the SMNRA, hypothesizing that shrubs may be an important component to *P. palmeri* populations (Chapter 1). I then document the effects of shrubs on *P. palmeri* performance and its spatial patterning to generate hypotheses about their interactions (Chapter 2). The results suggest that shrubs reduced penstemon emergence but increase seedling survival (a seed-seedling conflict) resulting in a pattern of association in which *P. palmeri* survive almost exclusively under shrubs. Further, while shrubs had little effect on *P. palmeri* growth, the results suggest that shrubs inhibited its flowering but improved its fruit maturation. Seed-sowing and seedling transplant experiments suggested that shrub soils may help penstemon populations persist as seeds on the landscape during dry years and that when seedlings emerge, shrub soils also improve their survival (Chapter 3). I then provide a detailed description of the direct and indirect reproductive responses of penstemon to shrubs (Chapter 4). The results suggest that competition with shrubs reduced penstemon seed production, but shrubs simultaneously facilitated penstemon water "sufficiency" and altered its pollinators foraging behavior, indirectly increasing seed production. I conclude by discussing the importance of these studies, and studies of plant interactions in general, for helping land managers balance the objectives of fuel management while protecting desirable species (Chapter 5).

ACKNOWLEDGMENTS

My endless gratitude goes to Drs. Eugene Schupp and Steven Ostoja for the many hours they spent editing; their efforts greatly improved the organization and flow of these chapters. Dr. Schupp provided invaluable advice and encouragement during challenging situations and was active in the conception of these studies; his hands-off approach challenged me and allowed me to develop a sense of independence and confidence that will no doubt be critical as an ecologist. Dr. Steven Ostoja has essentially been my mentor throughout this process; I cannot thank him enough. Also, Susan Durham spent many hours discussing and implementing the generalized linear mixed models used in Chapter 2 and 3; she also reviewed some manuscripts and provided valuable commentary.

The United States Geological Survey Western Ecological Research Center was a major funder of this research; specifically, Dr. Steven Ostoja played an important role in obtaining field crew and vehicles and Dr. Matt Brooks was critical in providing fiscal resources for my wages, field crew, and vehicles. My adviser, Dr. Eugene Schupp, has also supported me for many years on graduate research assistantships, which were invaluable for me to live day to day. Sigma Xi provided a grant that was crucial for the carbon isotope analyses of Chapter 4.

Thanks to the United States Forest Service (for allowing us to use the Spring Mountains National Recreation Area for our research; specifically, thanks to Julia Richardson and Stephanie Phillips for permitting seed collection and experiments), the many AmeriCorp Student Conservation Association interns (who helped with transplanting, watering, and constructing flower and fruit coverings), and Undergraduate Research Assistants of the Schupp lab (Shannon Kay, Corrin Liston, and Kourtney Blanc), who spent many hours helping test the maturity of every seed counted in Chapter 4.

Steven Lee vastly improve my botany skills and made my days in the field more interesting and Drew Rayburn provided useful commentary for Chapter 3 and shared many interesting conversations and publications about facilitation. Michael Cleaver (USGS) helped with transplanting and watering (Chapter 3). Jan Summerhays assisted with processing tissue samples for carbon isotope discrimination (Chapter 4).

My friends and family were more than willing to assist in data collection. My wife, Rachel, sowed penstemon seeds with the utmost skill, volunteered her Jeep for field work, paid some of my tuition, and encouraged me every day. My brother Pete also supported my field efforts several times, along with my friends Adam Peragrim, who counted and sowed seeds and helped thin shrubs and construction mimics, and Michael Martinez, who helped with some initial surveys.

This thesis could not have been done without the love and support of my wife family and friends, thank you all for believing and encouraging me.

Jesse M. Poulos

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CHAPTER 1

INTRODUCTION

Positive (e.g., facilitation, mutualism) and negative (e.g., competition, allelopathy) interactions among plants occur simultaneously (Callaway 1995; Callaway and Walker 1997; Maestre et al. 2003) and the Stress Gradient Hypothesis (SGH) predicts that net species interactions are frequently positive under extreme abiotic conditions (Bertness and Callaway 1994). In arid and semi-arid regions, uniform patterning among plants is often due to competition for water while spatial associations (i.e. aggregation) among plants can arise through many processes (Fowler 1986). Reliable interpretation of the mechanisms underlying spatial association is challenging, especially when used without complementary experimental evidence (Lepš 1990), however, patterns of spatial association often indicate a history of facilitative interactions (Callaway 2007; Brooker et al. 2008; Rayburn et al. 2010). Plants are said to be ‘associated’ when they aggregate spatially (Lepš 1990) and disentangling the processes that generate these spatial associations is challenging, requiring experimental approaches that are often expensive and logistically constrained (Lepš 1990; Callaway 2007; McIntire and Fajardo 2009). In contrast, assessing the effects of spatial associations for the performance of suspected beneficiaries is relatively easy to assess, the studies reported here primarily focus on how association with shrubs influences the individual performance of the perennial forb *Penstemon palmeri* (Palmer’s beardtoungue), but patterns of spatial association among *P. palmeri* populations and shrubs are also described.

Since younger plants are often more vulnerable to hostile environments (Lambers et al. 2008), scientists generally study associational effects (i.e. the effects of being aggregated) by documenting seedling emergence and early seedling survival and/or growth of the presumed beneficiary. However, considering associational effects across many life-stages improves our understanding of the nature of plant interactions (Schupp 1995, 2007; Miriti 2006; Armas and Pugnaire 2009; Gómez-Aparicio 2009). For example, while the effects of competition on reproduction are well documented (Weiner 1988) the reproductive stage is often not considered in facilitation studies, resulting in an incomplete understanding of the role of facilitation for plant fitness (Brooker et al. 2008; Bronstein 2009) and demography (Griffith 2010). The studies reported here describe these potential size-dependent responses in their analyses and consider the potential for life-stage conflicts.

This research was conducted in the Spring Mountains National Recreation Area (SMNRA) of the Humbolt-Toiyabe National Forest in Clark County, NV. The Spring Mountains ascend from low desert floors (600 m) to the top of Mt. Charleston (3632 m) and are characterized by distinct vegetation zones associated with increasing elevation. Sites used in these studies were located within shrublands at elevations of 1600 m-2000 m; the communities consisted of a diverse mixture of shrubs and forbs.

In recent times, fire seasons have become more severe due to fuel accumulation from historic fire suppression practices, climate change, human expansion (Keane et al. 2010), and invasion of grasses yielding fine-fuels (Brooks et al. 2004; Brooks and Matchett 2006). Consequently, mechanical thinning treatments are often required to manage fire threats to human populations in the wildland urban interface (WUI) (Kalabokidisl and Philip 1998), yet little is known about the potentially adverse effects of such treatments on desirable species (Ostoja et al. 2010). In the SMNRA the United States Forest Service (USFS) has deemed human communities to be threatened by wild-fire due to fuel load accumulation that could hamper fire containment and/or evacuation efforts (USFS 2007). The Spring Mountains Hazardous Fuel Reduction Project (fuel reduction project) designated 800 hectares (2,000 acres) of continuous stands of vegetation to be subjected to a wide variety of mechanical fuel reduction treatments, ranging from pruning of individual trees to whole tree and shrub removal (Ostoja et al. 2010). While it is unknown what impact these treatments will have on endemic species, at least 8 species (5 plants and 3 butterflies) of the Multiple Species Habitat Conservation Plan (MSHCP) of Clark County, Nevada (RECON 2000), have been observed within the treatment boundaries (Ostoja et al. 2010). The MSHCP is designed to protect the rare and endemic plant and animal species found in Clark County by eliminating unmitigated habitat loss and fragmentation (RECON 2000). Unfortunately, little is known of the impacts of these treatments on species covered by the MSHCP ('covered' species). I posit that if shrubs facilitate covered plants or the host plants of covered butterflies by altering microhabitat conditions, then their removal could result in an unaccounted loss of habitat. This scenario is likely since woody species frequently facilitate other species in arid environments (Gómez-Aparicio 2009). However, without an understanding of how covered species directly and indirectly interact with shrubs, land managers will find it challenging to eliminate habitat loss of covered species while protecting the needs of human populations within the expanding WUI (Radeloff et al. 2005).

This thesis focuses on interactions between shrubs and Palmer's beardtongue (*Penstemon palmeri* A. Gray), one of many nectar host plants used by the endemic MSHCP-covered Spring Mountains Acastus Checkerspot butterfly (*Chlosyne acastus* ssp *robusta*) (Boyd and Austin 2000). Yellow rabbit brush (*Ericameria viscidiflorus)* is this butterfly's only known larval host plant (Boyd 2004), while a suite of plant species have been observed to provide it nectar (see Boyd and Austin 2000; RECON 2000; reviewed in Ostoja et al. 2010; Pinyon Environmental Engineering Resources Inc. 2011). The removal of *E. viscidiflorus* will negatively affect *C. acastus* populations by eliminating its larval foodplant, but removing other shrub species might also indirectly influence *C. acastus* if shrubs facilitate productivity of *E. viscidiflorus* or the pollen and nectar productivity of its nectar host plants. However, it should be recognized that *C. acastus* use many other species for nectar and the sites considered occur below the elevation of their known populations (Pinyon Environmental Engineering Resources Inc. 2011).

Palmer's penstemon (*P. palmeri*) is a drought and cold tolerant native perennial forb occurring throughout much of the western United States (Cronquist et al. 1984). Seeds are highly sensitive to abiotic conditions (light, moisture, and temperature) during and after maturation and generally germinate in spring, though fall germination can occur rarely (Kitchen 1988; Allen and Meyer 1990; Kitchen and Meyer 1992; Meyer and Kitchen 1992). Although it is generally described as preferring disturbed washes with well drained soils (Cronquist et al. 1984), in the SMNRA populations can exist outside of active washes, co-occuring with mixed shrub communities. At lower elevations (1600 m -2000 m) they appear to grow mostly beneath shrub canopies (personal observation), possible indicating a history of positive interactions between shrubs and *P. palmeri*.

Using a combination of observational and experimental approaches, this research dynamically describes spatial associations between shrubs (i.e., potential facilitators) and *P. palmeri* (i.e., hypothesized beneficiary) and documents the effects of those associations on the performance of *P. palmeri* (emergence, survival, growth, and reproduction). In Chapter 2, an observational approach compares natural patterns of emergence, survival, growth, and reproduction of *P. palmeri* occurring in 'shrub' microhabitats versus 'interspace' microhabitats. It is expected that the observed influence of shrubs on *P. palmeri* will depend on the performance metric used as well as the life-stage and size of the individual (Brooker et al. 2008; Gómez-Aparicio 2009), but that at least some performance metrics will be improved by shrubs. In Chapter 3, an experimental approach was used to describe the importance of shrub canopies versus the shrub-associated soils in determining emergence and survival of sown *P. palmeri* seeds and the survival of transplanted seedlings. In Chapter 4, an observational study describes the direct and indirect effects of a single shrub species, *Eriodictyon angustifolium* (Nutt.), on *P. palmeri* seed production; this chapter used structural equation modeling to explore the importance of plant-plant interactions and plant-pollinator interactions for seed production in *P. palmeri*.

Lastly, in chapter 5, the theoretical and land management policy implications of chapters 2-4 are discussed in the context of the WUI that exists within the SMNRA.

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CHAPTER 2

EFFECTS OF SHRUBS ON A NATIVE PERRENIAL FORB’S (*PENSTEMON PALMERI* A. GRAY) INDIVIDUAL SURVIVAL, GROWTH, AND REPRODUCTION AND THE SPATIAL PATTERNING OF ITS POPULATIONS

I. Abstract

In arid and semi-arid shrublands the positive (e.g. facilitative) effects of shrubs often outweigh their negative (e.g. interspecific competitive) effects on understory species emergence and subsequent performance. These net-positive effects can produce spatial association of understory plants with shrubs. The balance between facilitative and competitive effects of shrubs on associated understory plants depends on, among many other factors, shrub species identity and the size and life-stage of understory plants. For example, this balance can shift from being net-facilitative at early life-stages (emergence, seedling and juvenile survival) to net-competitive at later life-stages (growth and reproduction). This study attempted to (1) describe interspecific spatial patterns (associative, no different than random, or dissociative) between the understory forb *Penstemon palmeri* and multiple shrub species and (2) document the effects of shrub-association on *P. palmeri* survival, growth, and reproduction. Shrubs had conflicting effects on *P. palmeri*, facilitating some performance metrics (emergence in 2011, survival, and buds-to-fruit maturation rates) but interfering with others (emergence in 2010, growth, and the probability of initiating reproduction). The effects of shrub-association on survival and reproduction were often size-dependent; shrub-association appeared to improve survival more for smaller *P. palmeri*. In contrast, shrub-association improved bud-to-fruit maturation mostly for larger *P. palmeri* but reduced the probability that smaller individuals would initiate reproduction. These conflicting effects of shrub-association coincided with population-level shifts in associative patterns; *P. palmeri* populations were initially associated with shrubs, but in 2010 shrubs reduced *P. palmeri*

emergence densities compared to interspaces and interspecific spatial patterns between shrubs and *P. palmeri* populations shifted from associative to dissociative. However, while shrubs had a net negative effect on the density of seedling emergence, the net positive effect on seedling survival gradually shifted interspecific spatial patterns toward associative. These results suggest that shrubs have important and complex effects on the spatial patterning and demography of *P. palmeri* populations, highlighting the importance of observing the effects of shrub-association temporally over a range of plant sizes, life-stages, and years.

II. Introduction

Positive (facilitation, mutualism) and negative (resource competition, allelopathy) interactions often occur simultaneously among plants (Callaway 1995, 2007 pp 179–254; Maestre et al. 2003). The stress gradient hypothesis (SGH; Bertness and Callaway 1994) posits that the effects of facilitation should frequently outweigh the effects of competition in physiologically stressful environments. Shrubs frequently ameliorate the stressful conditions that limit plant establishment in deserts, leading to many accounts of spatial association between shrubs and other species in arid environments (e.g. Flores and Jurado 2003). Many mechanisms can promote establishment beneath shrub canopies. For example, shrubs can buffer air and soil temperatures, improve soil nutrients and water availability, and offer protection from larger herbivores (Pugnaire and Lázaro 2000; Callaway 2007 pp 15-178). Thus, shrubs can be considered as ‘benefactors’ to the ‘beneficiary’ understory plants (Callaway 1995). In contrast, interspaces between shrubs can be characterized by intense insolation and extreme fluctuations in abiotic conditions (Tracol et al. 2011) which can directly or indirectly reduce emergence and/or survival, potentially limiting plant establishment (Callaway 1992; Callaway et al. 1996; Carrillo-Garcia et al. 2000; Kitzberger et al. 2000; Shumway 2000; Gómez-Aparicio et al. 2005; Becerra and Bustamante 2011). However, interaction can extend beyond the canopy to influence interspace-associated plants (Dawson 1993; Scholes and Archer 1997; Dickie et al. 2005). For example, hydraulic lift (sensu Richards and Caldwell 1987) can redistribute water from deep soil profiles making it available to plants with shallower roots (Caldwell and Richards 1989). These positive interactions can weaken with increasing distance from the lifting plant (Dawson 1993). Additionally, shade extends beyond the canopy on its poleward side. Thus, if hydraulic lift or shade improve recruitment or survival, then plants in interspaces may aggregate near shrubs even if they live beyond the canopy.

Interspecific spatial patterns (sensu Lepš 1990) between plants have long been assumed to give insight into the relative importance of positive versus negative interactions (Shreve 1931; Went 1942; Niering et al. 1963; Turner et al. 1966; Fowler 1986; McAuliffe 1988; Callaway 1995; Flores and Jurado 2003). However, using spatial patterns alone to infer their underlying processes has limitations (Lepš 1990; McIntire and Fajardo 2009) because other processes besides facilitation can create association among plants (Lepš 1990; McIntire and Fajardo 2009). For example, sub-canopy seed accumulation (Reichman 1984; Pugnaire and Lázaro 2000; Vander Wall and Thayer 2001; Bullock and Moy 2004) and shared habitat requirements in a patchy resource environment (Couteron and Kokou 1997) can lead to association among plants. Analyses of interspecific spatial patterns rely on correlative evidence and associative patterns are often driven by multiple dynamic processes; thus, when used alone, they cannot demonstrate the mechanisms that produced them, especially if they are statically observed (Lepš 1990). However, combining repeated measures of spatial pattern and understory plant performance (e.g. survival, growth, reproduction) provides more suggestive evidence than ‘snap shot’ correlative results (Lepš 1990; e.g. Chapter 3 herein).

Overstory species often have conflicting effects on their associated understory species emergence, survival, and growth, increasing some and decreasing others (Greenlee and Callaway 1996; Ibáñez and Schupp 2002; Miriti 2006; Gómez-Aparicio 2009; Soliveres et al. 2010). Such life-stage conflicts seem to be widespread (Schupp 2007). Thus, the observed effect of overstory plants on understory plants depend on the life-stage considered and performance metric used (Gómez-Aparicio 2009). One common type of life-stage conflict, the seed-seedling conflict, occurs when the conditions that favor seed success disfavor seedling success, and vice versa (Schupp 1995). Another common life-stage conflict occurs when overstory plants facilitate understory emergence and survival, but impede growth (Gómez-Aparicio 2009), probably because net-interactions often shift from being facilitative for the smaller and vulnerable seed and seedling stages to competitive as understory plants grow larger (Greenlee and Callaway 1996; Miriti 2006; Callaway 2007 pp 179-254). Since plant size is closely related to life-stage, others have similarly noted the importance of the sizes of interacting plants in determining the net effect of their interactions since smaller, more shallowly rooted understory plants are expected to benefit more from ameliorated stressful conditions (Callaway and Walker 1997). Thus, the direction and strength of the net interaction is expected to shift as understory plants develop and optimal conditions for survival and growth change.

The magnitude and direction of the net effects of interactions between plants is often species-specific, depending on characteristics of the benefactors (Callaway 2007 pp 117–178) and beneficiaries (Maestre et al. 2009; Reisner 2010). Different shrub species can have different effects on beneficiary germination (Rudgers and Maron 2003), survival (Callaway and D'Antonio 1991; Rudgers and Maron 2003; Landero and Valiente-Banuet 2010), productivity (Landero and Valiente-Banuet 2010), and reproduction (Casper 1996). Thus, each shrub species may uniquely alter conditions so as to create a heterogeneous patchwork of microhabitats with dissimilar effects on understory plants of various life-stages.

While the role of competition on reproduction is well documented (Weiner 1988), most research on facilitation has evaluated emergence and early survival and/or growth of beneficiary plants (Brooker et al. 2008). Although seedling survival may be improved under shrubs, slower vegetative growth and different reproductive patterns may be a consequence of higher densities of conspecifics under shrubs as well as competition with the facilitating shrub itself (Weiner 1988; Miriti 2006). Fluctuating abiotic conditions and competition influence how plants balance resource allocation between growth, maintenance, and reproduction, while investing in growth has the advantage of increasing future reproductive output, plants growing under these conditions may benefit from early reproduction rather than waiting and risking mortality or increasing interference by other plants if resources become more limited (Stearns 1976; Reekie and Bazzaz 2005; Bonser and Aarssen 2009). However, the timing of and allocation to reproduction in the context of microhabitat conditions have been rarely considered (but see De Ridder and Dhondt 1992a; b), especially in light of facilitation (Brooker et al. 2008), although studies of reproductive facilitation are becoming more common (Casper 1996; Shumway 2000; Tielbörger and Kadmon 2000; Choler et al. 2001; Kikvidze et al. 2001; Tirado and Pugnaire 2003; Griffith 2010; Soliveres et al. 2010; Cranston et al. 2012). Further, although the importance of size in reproduction is increasingly being recognized (Bonser and Aarssen 2009; Weiner et al. 2009), most studies examining potential facilitation of reproduction do not use size as a covariate of reproduction in their analyses (but see Soliveres et al. 2010; Cranston et al. 2012). The effects of facilitation on individual reproduction are important to consider since they can have emergent demographic effects at the population level (Griffith 2010). Despite the potentially complex effects of positive and negative interactions on beneficiary reproductive output and allocation patterns (e.g. Cranston et al. 2012), these topics have received little attention (Brooker et al. 2008).

This chapter describes interspecific spatial patterns between shrubs and the perennial forb *Penstemon palmeri*(A. Gray) in the Mojave Desert and examines the effects of different shrub species on multiple performance metrics, life-stages, and sizes of *P. palmeri* from 2008-2011. Specific objectives of this study were to: (1) characterize interspecific spatial patterns between shrubs and different cohorts and populations of *P. palmeri* over time, and (2) to evaluate the effects spatial association have on individual *P. palmeri* at multiple life-stages (emergence, survival, growth, and reproduction) and sizes. Predictions for Objective 1 are that: (1a) interspecific spatial patterns between cohorts of *P. palmeri* and shrubs will initially be associative, (1b) the existence and strength of *P. palmeri* association with shrubs will depend on the shrub species considered, (1c) interspace-associated *P. palmeri* will aggregate closer to shrubs than expected by chance, and (1d) interspecific spatial patterns between shrubs and *P. palmeri* will shift over time. Predictions for the second objective are that: (2a) shrub-association will have positive effects on *P. palmeri* survival, especially for the smallest individuals, (2b) *P. palmeri* survival will depend on the identity of the associated shrub, (2c) higher survival of shrub-associated individuals will result in increasingly strong associative patterns between *P. palmeri* and shrubs, (2d) the observed effect of shrub-association will depend on the performance metric evaluated (emergence vs. survival vs. growth vs. reproduction), and (2e) the size of *P. palmeri*. Still considering the second objective, predictions on the effects of shrub-association on emergence densities, plant size and growth are not clear. Further, the reproductive effects of shrub-association are difficult to predict based on the available literature. However, I ask four questions related to reproduction. After controlling for plant size, does shrub-association influence an individual’s (a) probability of initiating reproduction, (b) number of initiated buds, (c) percentage of initiated buds that successfully developed into mature fruits, and/or (d) total number of mature fruits?

III. Materials and Methods

This study was conducted in the mid-elevation (~1600 m) shrublands of the Spring Mountains National Recreation Area (SMNRA) in southern Nevada, USA. The SMNRA is within the Humboldt-Toiyabe National Forest and rises from Mojave Desert valleys at elevations below 600 m to 3,633 m at the alpine peak of Mt. Charleston. All plant names follow the USDA NRCS PLANTS database (NRCS 2011).

The suspected beneficiary is Palmer's beardtongue (*P. palmeri*), a short lived perennial herb common in washes and along roadsides throughout the arid south-western United States (Cronquist et al. 1984). It is considered to be drought and cold tolerant (NRCS 2011). Temperature and moisture during seed maturation and after dispersal drive germination requirements and dormancy induction and release (Kitchen and Meyer 1992) leading to cyclic patterns of seed dormancy and the formation of persistent seed-banks (Meyer and Kitchen 1992). At the start of the study, almost all *P. palmeri* appeared *a priori* to be found under shrub canopies. This observation was interpreted to suggest that shrub-induced facilitation may be influencing spatial patterning of *P. palmeri* populations.

Replicate study plots (16 m x 8 m) were established at three Mojave Desert shrubland sites within the SMNRA: Lovell Canyon (LC), Lower Kyle Canyon (LKC), and Middle Kyle Canyon (MKC). Distances between sites were between 5 km (LKC to MKC) and 14 km (LKC to LC). Plots were established within known patches of *P. palmeri* and plots in a site were at least 15 m apart. On 15 November 2008, eight plots were established in LKC and three plots were established in MKC. On 29 May 2009, three more plots were established in LC in an area that burned on 17 July 2002. Although sites were chosen to be similar (i.e. areas with slope < 5°; shrub dominated), they were analyzed separately since there remained considerable differences in soils and climate (Table 2-1), as well as shrub composition. Total shrub cover was approximately 56% (LC), 53% (LKC), and 62% (MKC); at MKC a single *Pinus monophylla* tree covered 4.9% of the considered area and was treated as a shrub for analyses. The shrub community at LC was dominated by *Eriodictyon angustifolium* (~70% of shrub cover) with a mixture of 10 other shrub species, at LKC was dominated by *Ericameria nauseosus* (~32% of shrub cover) with a mixture

Table 2-1
Mean annual precipitation (MAP), mean annual temperature (MAT) from 2000-2007, and soil association from lowest to highest precipitation (and highest to lowest MAT). Sites are shown below by location and according to elevation (elev.). Precipitation and MAT were obtained from (PRISM Climate Group 2010) and soil associations were obtained from the USDA NRCS web soil survey (Soil Survey Staff et al. 2011)

Site	**Location (latitude/longitude)**	**Elev. (m)**	**MAP† (mm)**	**MAT† (°C)**	**Soil Association**
LC	36° 9' 11.663" N/115° 34' 19.515" W	1770	334.18	12.05	Purob-Irongold††
LKC	36° 16' 18.867" N/115° 31' 17.328" W	1651	350.57	11.4	Purob-Irongold††
MKC	36° 16' 20.889" N/115° 34' 38.521" W	1967	415.53	3.75	Kylecanyon-Goodwater†††

† Years 2000-2007
†† frost-free period: 130-240 days; depth to petrocalcic layer: 36-51 cm
††† frost-free period: 90-180 days; depth to petrocalcic layer: 51-99 cm

of 8 other shrub species, and at MKC was dominated by *Artemisia tridentata* (~49% of shrub cover) along with 5 other shrub species.

Data for maximum temperature, minimum temperature, and precipitation were obtained for 2000-2011 for each site (PRISM Climate Group 2011). From 2000-2007, mean annual precipitation (MAP) and mean annual temperature (MAT) were inversely related and formed a subtle climatic gradient; LC was driest, with LKC being slightly wetter and MKC being the wettest (Table 2-1). Precipitation generally peaked during winter (November-March) and was followed by a pronounced dry season (April-Mid July), varying intensities of monsoons (July – September), and intermediate precipitation (September-November). Across all sites, winter precipitation during this study (2008-2011 mean = 313.3 mm) was more than the 2000-2007 winter average (mean = 211.7 mm). In contrast, monsoon precipitation in 2009 (63.7 mm) and especially in 2010 (25.7 mm) was less than average (83.6 mm). The highest site was colder and its frost-free period was shorter than at the other sites (Table 2-1).

Study design

At each site, interspecific spatial patterns between shrubs and *P. palmeri* were characterized (objective 1), and seedling emergence, survival, growth, and reproduction were monitored from November 2008 to March 2011 (objective 2). Three cohorts were considered: a mixed size and life-stage cohort comprised of juveniles and adults found during the first census (November 2008 LKC and MKC; May 2009 LC) and two cohorts of similarly sized and aged seedlings that emerged in the spring of 2010 and of 2011; there was no emergence in 2009. After the initial census, monitoring was conducted in May, July, and November 2009; May, July, and September 2010; and May 2011. During each census survival and size of previously tagged individuals were recorded. New recruits were tagged and their size (number of leaves) and microhabitat association (shrub-associated or interspace-associated) were recorded. An individual *P. palmeri* was considered to be shrub-associated if its stem originated below the shrub canopy, otherwise it was classified as being interspace-associated. For the initial mixed ‘2008 cohort’, measurements of the major diameter, the diameter perpendicular to the major, and height from ground level to rosette top were taken during each census. The number of reproductive nodes was counted and developmental stage (e.g. buds, flowers, fruits) noted.

For objective 1, at each site I evaluated interspecific spatial associations (sensu Lepš 1990) between shrubs and *P. palmeri* populations over time (prediction 1a) and tested whether the existence and magnitude of *P. palmeri* association with shrubs differed among shrub species (prediction 1b). Species-specific shrub cover was determined by establishing 4 parallel 16-m transects spaced 2 m apart in each plot and estimating cover using line-intercept methodology, which measures the proportion of the transects intercepted by each shrub species. Prediction 1c is that *P. palmeri* occurring in interspaces are closer to shrubs than expected by chance. To evaluate this prediction, random points were created by generating 4 sets of 10 random numbers between

0.00 m and 16.00 m for each plot; in the field, a set of 10 random points was assigned to each of the 4 transects used to characterize shrub cover, and the distance from each random point to the canopy edge of the nearest shrub was measured. Similarly, I measured the distance between the center of each interspace *P. palmeri* and the canopy edge of the nearest shrub. Because densities of newly recruited seedlings were very high, this part of the objective was abandoned for the two cohorts of new recruits in favor of obtaining more samples for the survival analyses. Interspecific spatial associations were described for each census to assess whether they would shift temporally (Prediction 1d).

For objective 2, survival of *P. palmeri* was expected to be higher under shrubs than in interspaces, especially when comparing the smallest individuals (prediction 2a). Survival data were collected by recording the status (alive or dead) of each plant during each census; the species of shrub was also noted to address whether survival differences were species specific (prediction 2b). Spatial associations within each cohort were described at the end of the study for comparison to initial spatial associations (prediction 2c).The size of the initial cohort (above ground volume; *AGV*) was assumed to be log-normally distributed and modeled as the volume of an ellipsoid ($AGV = \frac{\pi abc}{6}$, where a is the major diameter, b is its perpendicular diameter and c is plant height). Estimates of AGV were used to parameterize the equation for relative growth rate ($RGR = \frac{[ln(AGV_{t_{n+1}}) - ln(AGV_{t_n})]}{[t_{n+1} - t_n]}$, where t_n = time at census n). Size of new recruits was measured as a count of their leaves. For reproduction, total initiated buds was estimated using the maximum observed reproductive nodes (pedicels), and total mature fruits was estimated by using the maximum observed fruits from May-July, 2009. These metrics were used to evaluate predictions that observed differences between microhabitats would depend on the performance metric considered (prediction 2d) and that differences would be size dependent (prediction 2e).

Analyses

To address prediction 1a, that higher proportions of *P. palmeri* populations would be shrub-associated more often than expected by chance, separate chi-square goodness of fit tests were conducted for each cohort at each site. This is a common approach (Lepš 1990) in which observed numbers of shrub-associated and interspace-associated *P. palmeri* are compared to expected numbers, calculated as the proportional cover of a microhabitat (shrub vs. interspace) multiplied by the total number of *P. palmeri* in the plot. Although plants were clustered within plots, in each analysis observed and expected counts were pooled across plots; I am not aware of any goodness of fit test that accommodates clustering of both observed and expected counts. I assessed whether interspecific spatial patterns between shrubs and *P. palmeri* populations depend on the identity of the shrub species (prediction 1b), again using chi-square goodness of fit tests. This was accomplished by excluding interspace-associated *P. palmeri* from the chi-square analysis and treating each shrub species as a distinct microhabitat. Some shrubs species (LKC: *Atriplex canescens, Sphaeralcea ambigua*; MKC: *E. angustifolium, Fallugia paradoxa*) were excluded from analyses of interspecific spatial patterns since they covered little plot area and were never associated with *P. palmeri*. Species-specific chi-squared tests only used data from the first census because of high mortality and were applied separately for each cohort and site. To address prediction 1c, that interspace-associated *P. palmeri* would aggregate closer to shrubs than would be expected by chance, the empirical distribution function (EDF) of distance between *P. palmeri* and nearest shrub canopy edge was compared to the EDF for random points with the Kolmogorov-Smirnov test for Two Independent Samples (Smirnov 1939) using the NPAR1WAY procedure in SAS 9.2 (SAS Institute Inc. 2008); these data were again pooled over plots within each site. Finally, to determine whether interspecific spatial patterns shifted from census to census (prediction 1d), cohorts were combined within sites and chi-square goodness of fit tests were conducted for each census.

Shrubs were expected to improve *P. palmeri* survival, especially for the smaller *P. palmeri* (prediction 2a), and survival was predicted to depend on shrub species (prediction 2b). To test these predictions, survival analyses of the 2008 and 2010 cohorts were conducted using Cox proportional hazards (PH) models with the PHREG procedure in SAS 9.3 (SAS Institute Inc. 2011). Cox PH and standard regression models are similar. However, three key differences are: (1) individuals surviving past the last census are right-censored (allowing the fact that they survived to the last census to be accounted for in the estimates), (2) imprecise knowledge of when mortality occurred between censuses can be accounted for by treating data as “tied”, and (3) estimates are in the form of easily interpreted Hazard Ratios (HR), which represent comparisons of survival between one group (numerator) relative to another group (denominator) (e.g. interspaces versus shrubs) (Allison 2010). For all survival models, potential non-independence among individuals within plots was accounted for with a shared frailty model for plants within plots using the ‘random’ statement within PROC PHREG; ties in the data (see ‘2’ above) were addressed using the ‘exact’ method, which is recommended when the precise time of death between censuses is unknown (Allison 2010). Six survival models (3 sites × 2 cohorts per site; survival data were not collected for the 2011 cohort) were used to examine the survival effects of shrub-association. Mortality risk was modeled as a response to an individual’s initially observed size, spatial pattern (shrub-associated or interspace-associated), and their interaction. To address species-specific effects of shrubs on *P. palmeri* survival (prediction 2b), six more Cox models were used to examine pair-wise comparisons of shrub effects on hazard of *P. palmeri* for both cohorts within each site (e.g. survival under species ‘A’ versus species ‘B’, species ‘B’ versus species ‘C’, etc.); species with fewer than 10 associated *P. palmeri* were excluded from the analysis. To determine whether differences in survival between shrub and interspace microhabitats coincided with shifts in interspecific spatial patterns within cohorts (prediction 2c), chi-squared goodness of fit tests from the final census were compared to those of the initial census.

To assess whether shrubs affected size, growth, and reproduction (prediction 2d) and whether the effects were size-dependent (prediction 2e), differences in *P. palmeri* size, growth, and reproduction between shrub-associated and interspace-associated plants were analyzed using generalized linear mixed models (GLMM) with the GLIMMIX procedure in SAS 9.2 (SAS Institute Inc. 2008).When possible, models included random effects for plots and their interaction with microhabitat to account for within plot dependence. To model size ($\log_{10} AGV$) and growth (*RGR*) I included a fixed effect factor for microhabitat association; size was modeled as log-normal distributed while *RGR* was modeled as normally distributed. For the 2008 cohort at LC, size at only the first census was analyzed and growth only between the first and second censuses was analyzed since sample sizes of interspace-associated plants were too small in the subsequent censuses to meaningfully analyze. At LKC and MKC in 2008 there were too few interspace-associated plants to conduct reliable analyses of size and growth. For the 2010 cohort at all sites, cohort analyses of size were made only for the first census and growth was not analyzed because of poor survival. For the four questions related to reproduction, initial plant size ($\log_{10}(AGV)$), microhabitat association (shrub or interspace), and their interaction were used as fixed effects factors. Response data for each reproductive question were distributed differently; assumed distributions for questions a-d were binary, negative-binomial, over-dispersed binomial, and negative-binomial, respectively. For questions b-d, only plants that initiated reproduction were analyzed. Insufficient numbers of *P. palmeri* in interspaces at LKC and MKC (all years) precluded reliable analysis of reproduction. Only the initial cohort (2008) at LC was evaluated for these questions since new recruits did not become reproductive during this study and the other two sites (LKC and MKC) had too few reproductive plants in the initial cohort. However, at LC the presence of 32 reproductive interspace-associated plants and 108 shrub-associated plants permitted comparisons of reproduction in 2009; unfortunately, robust analysis of reproduction at LC was not possible in 2010 due to low densities of *P. palmeri* in interspaces (2 remaining; 10 fruits produced in interspaces and 177 fruits produced under shrubs). Finally, random effects were included only for plots; ideally, models would have also included random effects for the plot × microhabitat interaction, but there were issues with their estimation and they were not included.

IV. Results

For the 2008 cohort, a total of 238 (LC; 0.62 plants/m^2), 99 (LKC; 0.10 plants/m^2), and 69 (MKC; 0.18 plants/m^2) plants were tagged and monitored. No emergence occurred in 2009; emergence did not occur until the spring of 2010 and these seedlings were tagged in July 2010; 500 (LC; 1.30 plants/m^2), 60 (LKC; 0.06 plants/m^2), and 73 (MKC; 0.19 plants/m^2) newly recruited seedlings were tagged and monitored. Finally, in 2011 another cohort emerged, yielding 597 (LC; 1.55 plants/m^2), 191 (LKC; 0.19 plants/m^2), and 265 (MKC; (0.69 plants/m^2) new seedlings. Since ages are relatively similar within cohorts of new recruits, their size varied much less than did the sizes of the 2008 mixed-age cohort, which likely consisted of the surviving plants of many previous recruitment events.

Objective 1: temporal descriptions of interspecific spatial patterns

Prediction 1a: At the first census (Nov. 2008 at LKC and MKC; May 2009 at LC, interspecific spatial patterns varied between cohorts, but were relatively consistent within cohorts and between sites (Fig. 2-1). For the 2008 cohort, interspecific spatial patterns between shrubs and *P. palmeri* populations were associative at all sites during the initial census (Fig. 2-1); there were significantly more shrub-associated juveniles and adults than would be expected based on shrub cover (all sites $P < 0.001$; LC: $\chi^2_1 = 66.89$; LKC: $\chi^2_1 = 55.59$, MKC: $\chi^2_1 = 22.28$). For the

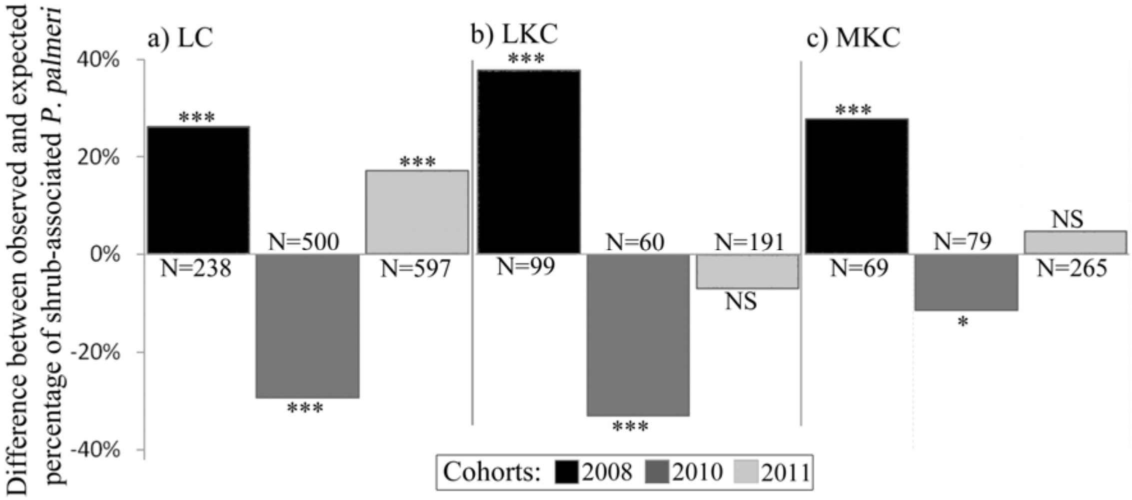

Fig. 2-1: Initial differences between the proportion of shrub-associated *P. palmeri* observed compared to the proportion expected based on shrub cover for each cohort (shades) and site (panels a-c). N=total number of *P. palmeri* individuals. Significance measures result from chi-squared goodness of fit tests (*** P < 0.001; * P < 0.05; NS: Not Significant).

2010 cohort, interspecific spatial patterns were dissociative during the initial census (July 2010) (Fig. 2-1); fewer emerged seedlings were shrub-associated than expected based on shrub cover at all sites (LC: $P < 0.001$, $\chi^2_1 = 178.93$; LKC: $P < 0.001$, $\chi^2_1 = 26.78$; MKC: $P = 0.037$, $\chi^2_1 = 4.35$). For the 2011 cohort, interspecific spatial patterns were associative at LC during the initial census (May 2011) (Fig. 2-1a); more seedlings were shrub-associated than expected based on shrub cover ($P < 0.001$; $\chi^2_1 = 73.53$). In contrast, interspecific spatial patterns were neither associative nor dissociative (i.e., were not statistically different than random) at LKC (Fig. 2-1b; $P = 0.060$; $\chi^2_1 = 3.55$) and MKC (Fig. 2-1c; $P = 0.128$; $\chi^2_1 = 2.31$); at these sites seedlings emerged under shrubs in proportion to shrub cover.

Prediction 1b: Shrub-associated *P. palmeri* occurred in proportions greater than expected under some shrub species, in proportions lower than expected under others, and in proportions no different than expected under the remaining species (Fig. 2-2). For shrub-associated *P. palmeri* of the 2008 cohort, differences among shrub species in their associations with *P. palmeri* were strong at LKC and MKC, but at LC the pattern was weaker and only marginally significant (Fig.

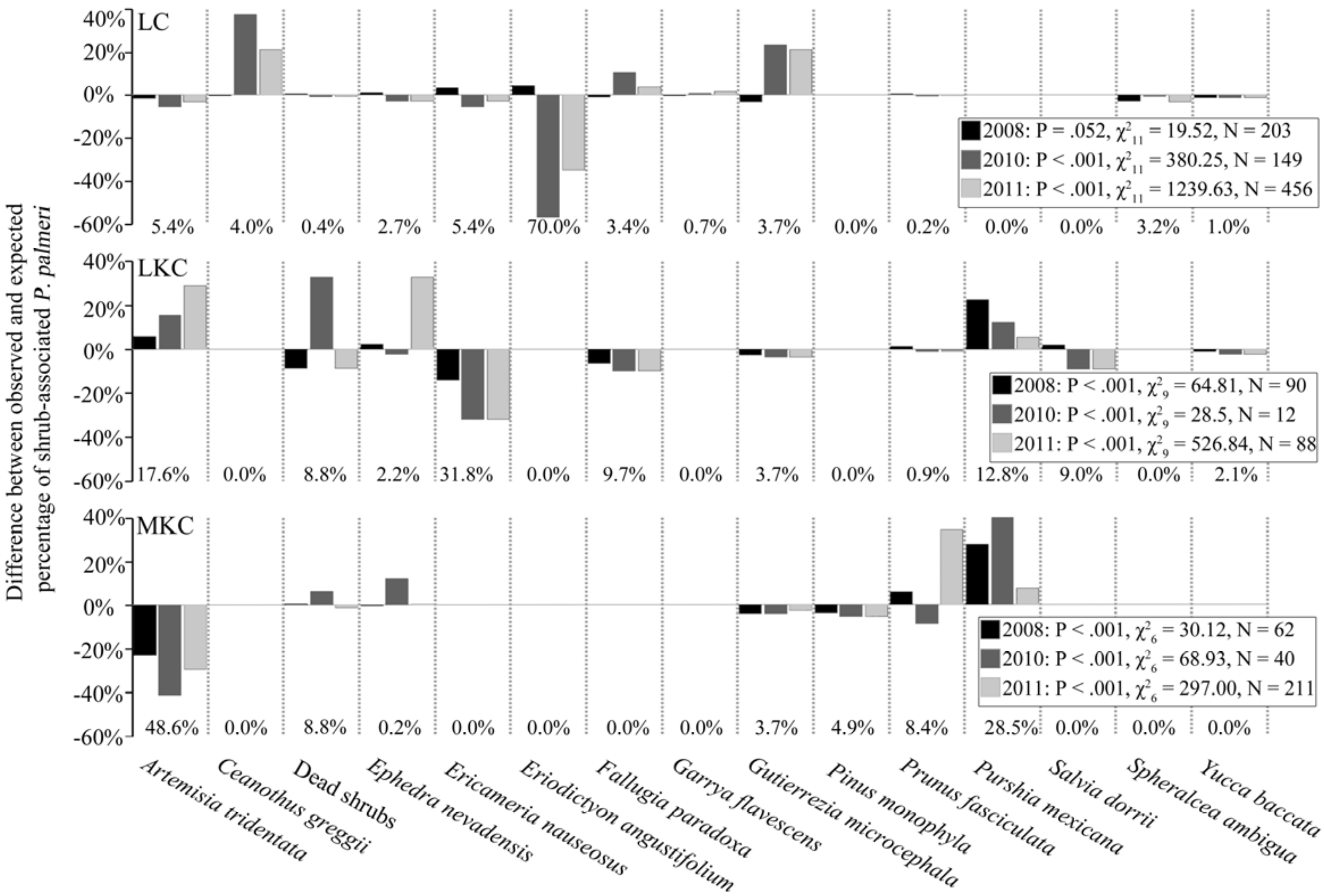

Fig. 2-2: Species specific differences between observed and expected percentage of shrub-associated *P. palmeri* (%; Y-axes) at LC (top panel), LKC (middle panel), and MKC (bottom panel). Significance test results from chi-square goodness of fit tests are reported in boxes. Percentage of shrub cover for each species are noted along the X-axis for each site.

2-2). At LKC, the 2008 cohort of *P. palmeri* was most strongly associated with *P. mexicana* and most strongly dissociated with *E. nauseosus* (Fig. 2-2, middle panel). At MKC, *P. palmeri* were also most strongly associated with *P. mexicana* but were most strongly dissociated with *A. tridentata* (Fig. 2-2, bottom panel).

In 2010, seedling emergence differed from expected emergence under at least some shrub species at all sites (Fig. 2-2). At LC, seedlings emerged at higher than expected densities under *C. greggii*, *F. paradoxa*, and *G. microcephala*, and in much lower than expected densities under *E. angustifolium* (Fig. 2-2, top panel). At LKC, seedlings emerged at higher than expected densities under *A. tridentata, P. mexicana,* and dead shrubs and at lower than expected densities under *F. paradoxa* (unlike at LC) and *E. nauseosus*; these patterns were similar to those in the initial cohort (Fig. 2-2, middle panel). At MKC, seedlings emerged at higher than expected densities under *P. mexicana* but at lower than expected densities under *A. tridentata* (contrasts LKC), again patterns similar to those in the initial cohort (Fig. 2-2, bottom panel).

For the 2011 cohort, at LC patterns of emergence were generally similar to those in the 2010 cohort, but appear less pronounced (Fig. 2-2, top panel). At LKC, seedlings were associated more strongly with *A. tridentata* and *E. nevadensis* (unlike in 2010) and more weakly with *P. mexicana* than the previous year (Fig. 2-2, middle panel), and at MKC, seedlings emerged at higher than expected densities under *P. fasciculata* (contrasts 2010) while seedlings showed weaker associations with *P. tridentata* than the 2008 and 2010 cohorts (Fig. 2-2, bottom panel).

Prediction 1c: Interspace-associated *P. palmeri* of the 2008 cohort occurred no different from random throughout interspaces; there was no statistically significant difference between the distances from shrub canopy edges to randomly generated points versus naturally occurring *P. palmeri* at any site (LC: $D = 0.083$, $P = 0.998$; LKC: $D = 0.184$, $P = 0.934$; MKC: $D = 0.482$, $P = 0.103$). As previously mentioned, this prediction was not addressed for new cohorts.

Prediction 1d: Interspecific spatial patterns between *P. palmeri* populations and shrubs changed over time (Fig. 2-3). The initial 2008 mixed age cohort had much higher than expected proportions of *P. palmeri* associated with shrubs at all sites, indicating strong associations between *P. palmeri* populations and shrubs. When the 2010 cohort emerged at higher than expected densities in interspaces, the proportion of *P. palmeri* that were shrub-associated sharply declined at all sites (Fig. 2-3); at LC and LKC this flush of new recruits in interspaces was so strong that it resulted in significantly fewer *P. palmeri* associated with shrubs than expected by chance (i.e., a shift from associative patterns to dissociative patterns) but at MKC the result was a shift from strong association with shrubs to patterning no different than random. Following 2010 emergence, from July-September, interspecific spatial patterns shifted back from dissociative to associative at LC and LKC and remained no different than random at MKC. When the 2011 cohort emerged, a drop in the proportion of shrub-associated *P. palmeri* was seen at LKC and MKC, similar to, but less pronounced than in 2010, resulting in small negative shift (Fig. 2-3). However, at LC, emergence in 2011 was higher under shrubs, increasing the proportion of shrub-associated *P. palmeri* and amplifying already associative interspecific spatial patterns (Fig. 2-3).

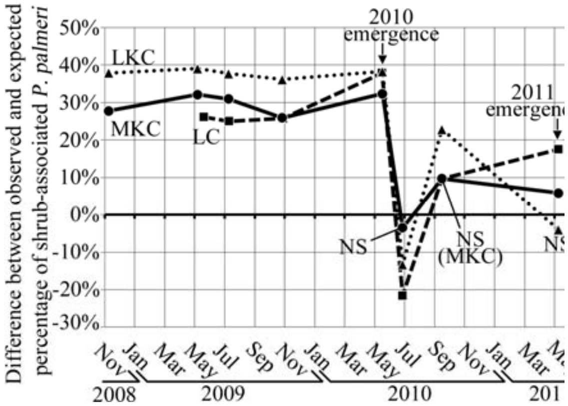

Fig. 2-3: Temporal comparison of the overall difference between the observed and expected percentage of shrub-associated *P. palmeri* when cohorts were combined within sites. ‘NS’ indicates point-comparisons that were no different than zero, all other points were significantly different than zero (P < 0.05).

Objective 2: evaluation of plant performance

Prediction 2a: Mortality was high across all sites and microhabitats (Fig. 2-4). For the initial 2008 cohort at LC, microhabitat association (shrub or interspace) and size of *P. palmeri* were important factors driving survival, but their interacting effects were less pronounced (Table 2-2). While the importance of the statistical interaction between size and microhabitat is questionable at LC, the HR estimates indicate greater survival of shrub-associated seedlings than interspace associated seedlings (i.e. HR < 1.00), but indicate no difference in survival rates between microhabitats for larger plants (Table 2-2). At LKC and MKC, microhabitat, plant size, and their interaction had little effect on the survival of the 2008 cohort (Table 2-2). For the 2010 cohort at LC, microhabitat was more important than size and the microhabitat-size interaction in driving seedling survival (Table 2-2). Further, while there is not statistical support that survival depends on size or its interaction with microhabitat, HR estimates indicate that shrub-associated seedlings had higher survival than those growing in

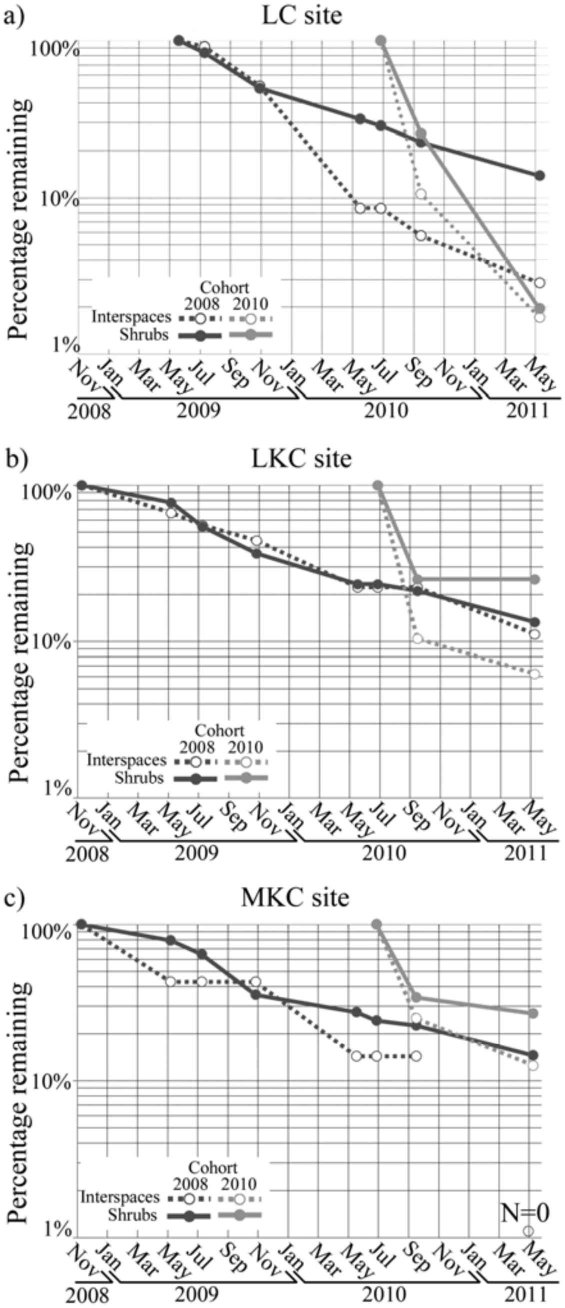

Fig. 2-4: Comparison of the proportion of shrub-associated (solid lines) and interspace-associated (dotted lines) *P. palmeri* remaining over time at (a) LC, (b) LKC and (c) MKC for the 2008, mixed cohort (black) and for the 2010 emerged seedling cohort (gray). Note that y-axes are on the $\log_{10}$ scale and the circles on the lines represent the time of each census.

Table 2-2

Model fit and hazard ratios (HR) and their 95% confidence limits for six Cox PH models (3 sites × 2 cohorts) with covariates for plant size (Log_{10}*AGV* for the 2008 cohort and Log_{10}(leaf count) for the 2010 cohort), microhabitat association (shrub or interspace), and their interaction. The HR represents the risk of mortality for shrub-associated *P. palmeri* relative to interspace-associated *P. palmeri*. HR > 1.0 indicates higher mortality for *P. palmeri* that are shrub-associated than interspace-associated while HR < 1.0 indicates the opposite. Size was Log_{10}*AGV* for the 2008 cohort and Log_{10}(leaf count) for the 2010 cohort.

Model Information			**Parameter Estimates**		**Hazard Ratios**			
Site	**Cohort**	**Model Fit**	**Covariate**	***P***	***AGV***	**HR**	**95% CL**	***P***
LC	**2008**	$\chi^2_{4.15}$=11.83	Microhabitat	0.049	64 cm^3	0.45	0.23-0.90	0.023
	Cohort	*P*=0.021	Size	0.035	640 cm^3	0.71	0.48-1.06	0.094
			Interaction	0.109	6400 cm^3	1.13	0.57-2.25	0.735
	2010	$\chi^2_{3.44}$=13.02	Microhabitat	0.073	2 leaves	0.57	0.37-0.88	0.010
	Cohort	P=0.007	Size	0.569	4 leaves	0.72	0.56-0.91	0.007
			Interaction	0.340	6 leaves	0.90	0.49-1.64	0.729
LKC	**2008**	$\chi^2_{8.02}$=19.52	Microhabitat	0.550	64 cm^3	1.12	0.34-3.67	0.848
	Cohort	P=0.013	Size	0.467	640 cm^3	0.59	0.10-3.40	0.551
			Interaction	0.526	6400 cm^3	0.31	0.01-11.33	0.520
	2010	$\chi^2_{3.00}$=9.30	Microhabitat	0.018	2 leaves	0.15	0.03-0.69	0.015
	Cohort	P=0.026	Size	0.014	4 leaves	1.04	0.39-2.79	0.940
			Interaction	0.033	6 leaves	7.24	0.63-82.85	0.112
MKC	**2008**	$\chi^2_{3.00}$=1.97	Microhabitat	0.680	64 cm^3	0.61	0.18-2.05	0.425
	Cohort	P=0.578	Size	0.907	640 cm^3	0.70	0.27-1.77	0.447
			Interaction	0.852	6400 cm^3	0.79	0.11-5.86	0.820
	2010	$\chi^2_{3.78}$=5.08	Microhabitat	0.243	2 leaves	0.44	0.14-1.39	0.160
	Cohort	P=0.282	Size	0.686	4 leaves	0.59	0.33-1.06	0.077
			Interaction	0.747	6 leaves	0.80	0.35-1.85	0.605

interspaces for the two smallest size classes but not for the largest (Table 2-2). At LKC, there was stronger evidence that survival was related to size, microhabitat and their interaction; when the smallest plants were compared, HR estimates indicate higher survival for shrub-associated seedlings than those located in interspaces, but HR estimates increased when larger seedlings were compared and indicate survival rates were becoming more similar between microhabitats for larger seedlings (Table 2-2). At MKC, there was little evidence that any of these factors were important drivers of survival (Table 2-2).

Prediction 2b: For the 2008 cohort, at LC there was evidence that the identity of the associated shrub influenced *P. palmeri* survival; the best support was seen when comparing *E. angustifolium*-associated *P. palmeri* to those associated with *E. nauseosus*, which had lower survival (Table 2-3). Note also that there was some indication that plants associated with *E. angustifolium* survived better compared to interspace-associated plants (Table 2-3). At LKC, the best evidence that survival was higher under one shrub species compared to another came when comparisons involved *S. dorrii*; note that relative to interspace-associated plants, there was little statistical support that association with any shrub species improved survival more than the others, though *S. dorrii* was the strongest candidate as benefactor to *P. palmeri* survival (Table 2-3). At MKC there was little evidence that microhabitat association was a major determinant of survival (Table 2-3). For the 2010 cohort, at LC there was little evidence that seedling survival varied between shrub microhabitats, instead, there is stronger evidence that multiple shrub species improved seedling survival relative to interspaces, but none improved survival more than the others (Table 2-3). At LKC, there were too few shrub-associated seedlings to make reliable comparisons of survival and at MKC only *P. mexicana* had sufficient numbers of shrub-associated seedlings for the analysis, and there was little evidence that this species influenced seedling survival relative to interspaces (Table 2-3).

Prediction 2c: After mortality occurred, the proportion of shrub-associated *P. palmeri* either remained higher than expected (2008 cohort) or shifted toward higher than expected (2010 cohort), indicating maintenance of or a shift in interspecific spatial patterns from dissociative to associative for both cohorts at all sites (Fig. 2-5). For the 2008 cohort, at all sites interspecific spatial patterns between shrubs and *P. palmeri* began as associative ($P < 0.001$; LC: $\chi^2_1 = 66.89$; LKC: $\chi^2_1 = 55.59$; MKC: $\chi^2_1 = 22.28$) and remained associative (LC: $\chi^2_1 = 16.72$, $P < 0.001$; LKC: $\chi^2_1 = 7.86$, $P = 0.005$; MKC: $\chi^2_1 = 5.44$, $P = 0.020$). Interspecific spatial patterns between the

Table 2-3

Results of six Cox PH models (3 sites × 2 cohorts), each with a ‘microhabitat’ variable specifying the species-specific association of *P. palmeri*. Only species with 10 or more associated *P. palmeri* were included and only significant comparisons are reported. Hazard ratios represent the risk of mortality for *P. palmeri* associated with the numerator microhabitat relative to the denominator microhabitat. When HR < 1.00, mortality is estimated to be lower for plants associated with the numerator microhabitat; when HR > 1.00 the opposite is true. *P*-values are reported for overall model significance (P_{M}), significance of specifies-specific microhabitat covariate (P_{SPP}), and the significance of pair-wise comparisons between microhabitats (P_{HR}).Bolding indicates significant at to 0.05 level.

Site	**Cohort**	**Model Fit**	**Species Compared**	**HR**	**95% CL**	**P_{HR}**
LC	**2008**	$\chi^2_{3.40}$=11.96	***E. angustifolium* ÷ *E. nauseosus***	**0.54**	**0.32-0.91**	**0.020**
		$P_{\mathrm{M.}}$=0.011	*E. nauseosus* ÷interspaces	1.35	0.72-2.51	0.352
			E. angustifolium ÷ interspaces	0.72	0.48-1.09	0.123
	2010	$\chi^2_{4.45}$=13.83	*C. greggii* ÷ *E. angustifolium*	1.15	0.67-2.00	0.613
		P_{M}=0.011	*C. greggii* ÷ *F. paradoxa*	1.20	0.69-2.09	0.528
			C. greggii ÷ *G. microcephala*	1.01	0.65-1.57	0.968
			***C. greggii* ÷ interspaces**	**0.70**	**0.52-0.95**	**0.021**
			E. angustifolium ÷ *F. paradoxa*	1.04	0.53-2.05	0.914
			E. angustifolium ÷ *G. microcephala*	0.88	0.49-1.58	0.658
			***E. angustifolium* ÷ interspaces**	**0.61**	**0.37-1.00**	**0.048**
			F. paradoxa ÷ *G. microcephala*	0.84	0.47-1.53	0.575
			***F. paradoxa* ÷ interspaces**	**0.59**	**0.35-0.97**	**0.036**
			G. microcephala ÷ interspaces	0.69	0.48-1.00	0.051
LKC	**2008**	$\chi^2_{7.95}$=21.05	*A. tridentata* ÷ *E. nauseosus*	1.58	0.73-3.42	0.248
		P_{M}=0.007	*A. tridentata* ÷ *P. mexicana*	1.58	0.84-2.99	0.159
			A. tridentata* ÷ *S. dorrii	**5.90**	**1.40-24.85**	**0.016**
			A. tridentata ÷ interspaces	1.46	0.47-4.59	0.516
			E. nauseosus ÷ *P. mexicana*	1.00	0.47-2.12	0.995
			E. nauseosus ÷ *S. dorrii*	3.74	0.90-15.57	0.070
			E. nauseosus ÷ interspaces	0.93	0.28-3.13	0.902
			P. mexicana ÷ *S. dorrii*	3.73	0.93-14.99	0.063
			P. mexicana ÷ interspaces	0.92	0.29-3.00	0.896
			S. dorrii ÷ interspaces	0.24	0.05-1.31	0.100
	2010	χ^2=NA	No species with 10 or more associated *P. palmeri*			
		P_{M} =NA				
MKC	**2008**	$\chi^2_{2.00}$=2.22	*A. tridentata* ÷ *P. mexicana*	0.73	0.37-1.42	0.350
		P_{M}=0.330	*A. tridentata* ÷ interspaces	0.49	0.19-1.26	0.140
			P. mexicana ÷ interspaces	0.68	0.29-1.56	0.357
	2010	$\chi^2_{1.64}$=2.42	*P. mexicana* ÷ interspaces	0.68	0.37-1.25	0.230
		P_{M}=0.230				

2010 cohort and shrubs shifted from dissociative at all sites (LC: $\chi^2_1 = 178.83$, $P < 0.001$; LKC: $\chi^2_1 = 26.78$, $P < 0.001$; MKC: $\chi^2_1 = 4.35$; $P = 0.037$) to no different than random at all sites (LC: $\chi^2_1 = 2.50$, $P = 0.114$; LKC ($\chi^2_1 = 0.03$; $P = 0.862$); MKC: $\chi^2_1 = 0.28$, $P = 0.596$).

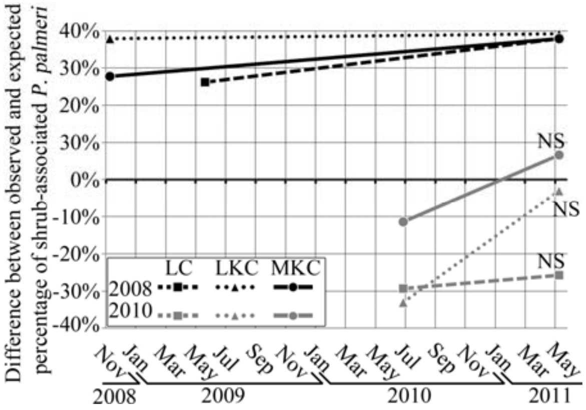

Fig. 2-5: Initial and final difference between the observed and expected percentage of shrub-associated *P. palmeri* across sites and cohorts. NS' indicates point-comparisons that were no different than zero; all other points were different than zero ($P < 0.05$)

Size and growth: For the 2008 cohort, initially observed plant size ($\mathrm{Log}_{10}AGV$; May 2009) did not appear to be different between microhabitats at LC (LC: $F_{1,2} = 0.46$, $P = 0.566$); comparisons of size and growth were not made for this cohort at MKC and LKC due to the scarcity of interspace-associated plants. At LC, *RGR* of the plants that survived through the second census (July, 2009; 49 days later) was estimated to be 3.46 times greater for interspace associated plants than for those associated with shrubs. However, there is little statistical support that this difference is meaningful ($F_{1,2} = 4.77$; $P = 0.161$). For the 2010 cohort at LC, analyses could not be blocked by plot since one of the three plots had no emergence and the other had only 4 shrub-associated seedlings emerge leaving only one plot with sufficient data for comparisons. Thus, data were pooled across plots at LC; pooling was not necessary at LKC and MKC. Given this, shrub-associated seedlings at LC were estimated to be ~7.4% larger during the first census (July 2010) than those associated with interspaces, but the statistical support for this difference was suggestive at best ($F_{1,501} = 3.20$; $P = .074$). At the other sites, there was less evidence that seedling size was different between microhabitats during the first census (LKC: $F_{1,1} = 0.16$, $P = 0.761$; MKC: $F_{1,1} = 1.05$, $P = 0.492$).

Reproduction: Flowering generally started in May, with most flowers senescing by the end of July and capsule maturation continuing through most of October. Recall that reproduction was only analyzed for the 2008 cohort at LC during the 2009 season (see '*Methods'*).

There was strong evidence that the probability of initiating reproduction (question a) was influenced by microhabitat association and plant size, but not their interaction (Fig. 2-6a). Despite the lack of statistical support for an interaction, the model estimated that for shrub-associated plants the probability of initiating reproduction in 2009 increased with increasing plant size ($F_{1,232} = 39.56$; $P < 0.001$), but size had no significant effect for interspace-associated plants ($F_{1,232} = 1.638$; $P = 0.200$) (Fig. 2-6a). The smallest of interspace-associated plants (~105 cm^3; $\log_{10}AGV = 2.02$) were estimated to be 69.9% more likely to reproduce than equal-sized shrub- associated plants ($F_{1,232} = 10.18$; $P = 0.002$). With increasing plant size, this difference remained statistically significant ($P < 0.05$) for plants up to an $AGV = 2500$ cm^3 ($\log_{10}AGV > 3.40$); plants of this size were 16.1% more likely to reproduce than equal-sized shrub-associated plants ($F_{1,232} = 3.88$; $P = 0.049$). When AGV exceeded 2500 cm^3 ($\log_{10}AGV > 3.40$), differences in the likelihood of initiating reproduction were insignificant and continued to decline (Fig. 2-6a).

Of the *P. palmeri* that initiated reproduction, the number of buds initiated (question b) was significantly positively influenced by plant size ($F_{1,134} = 100.98$; $P < 0.001$) but not by microhabitat association ($F_{1,134} = 0.98$; $P = 0.324$) or by its interaction with plant size ($F_{1,134} = 1.19$; $P = 0.277$). Although interspace associated plants appeared to initiate more buds, especially at the larger sizes (Fig. 2-6b), the difference was not statistically significant even for the largest ($AGV = 13{,}280$ cm^3; $\log_{10}AGV = 4.12$) of interspace-associated plants ($F_{1,134} = 2.16$; $P = 0.143$).

The proportion of initiated buds to successfully mature into fruits (i.e. bud-to-fruit maturation rate) (question c) was not significantly influenced by microhabitat ($F_{1,134} = 0.03$; $P = 0.873$) or plant size ($F_{1,134} = 0.59$; $P = 0.445$) alone, but was significantly influenced by their interaction ($F_{1,134} = 5.74$; $P = 0.018$). This interaction revealed that bud-to-fruit maturation rate

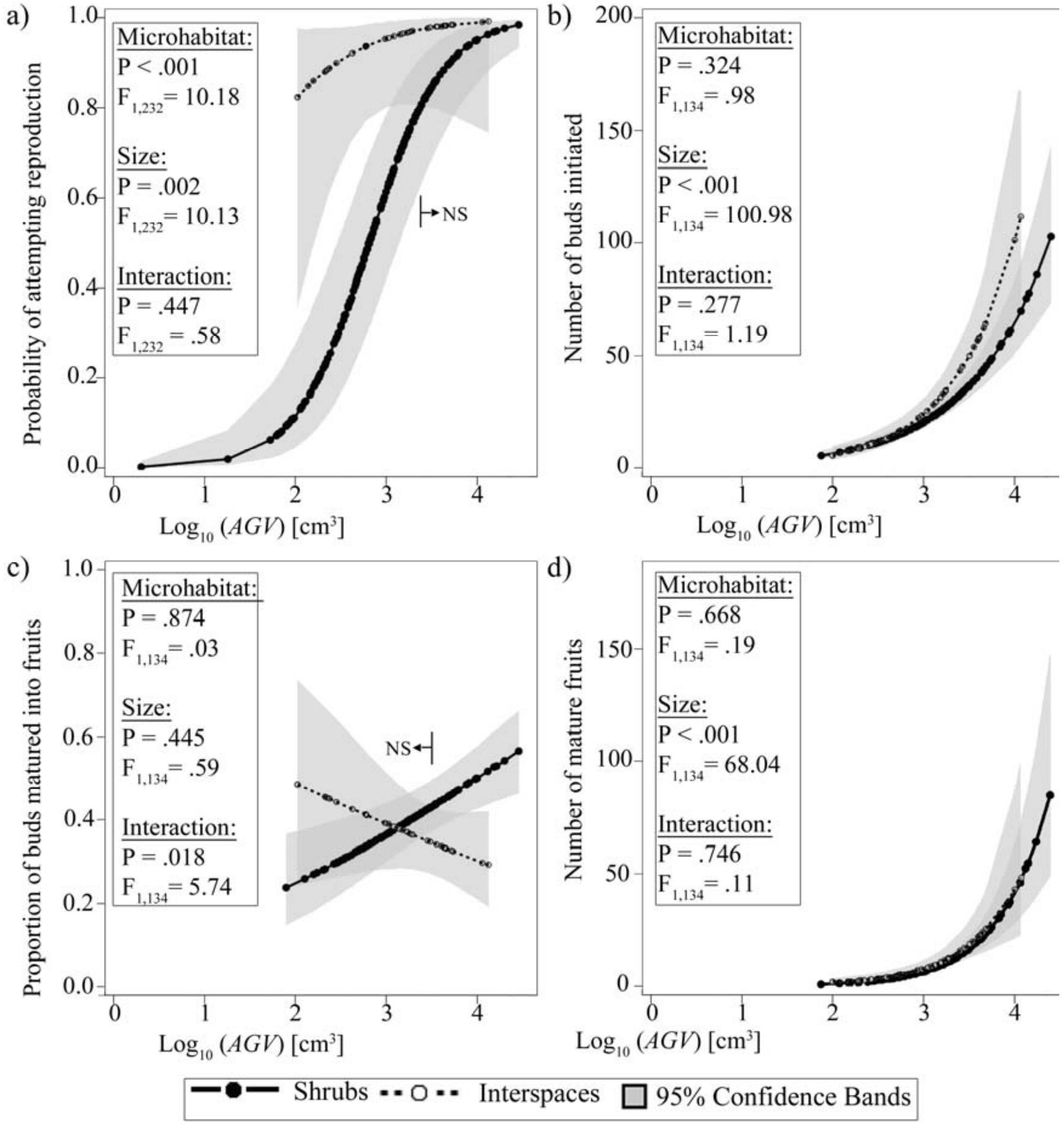

Fig. 2-6: GLMM predictions of four reproductive responses (y-axes) at LC in 2009 for shrub-associated (solid lines) and interspace-associated (dashed lines) different sized *P. palmeri*(x-axes): (a) the probability of initiating reproduction, (b) the number of buds initiated, (c) the proportion of buds matured into fruits, and (d) the number of mature fruits. Shaded regions are 95% confidence bands. All models included covariates for plant size (x-axes), microhabitat association, and their interaction. 'NS' indicates no significant difference ($P \geq 0.05$). Note that the reported estimates of microhabitat effects result from comparing average sized plants.

was independent of plant size for interspace-associated *P. palmeri* ($F_{1,134} = 0.83$; $P = 0.362$) but increased significantly ($F_{1,134} = 12.04$; $P < 0.001$) with increasing plant size for shrub-associated *P. palmeri* (Fig. 2-6c). Bud-to-fruit maturation rate was not significantly greater under shrubs than in interspaces until *AGV* exceeded 3800 cm^3 ($\log_{10}AGV = 3.58$ cm^3) after which bud-to-fruit maturation rate was between 8.82% ($F_{1,134}=3.92$; $P = 0.049$) and 20.9% ($AGV = 13{,}280$ cm^3; $\log_{10}AGV = 4.12$ cm^3; $F_{1,134}= 8.12$; $P = 0.005$) greater for shrub-associated plants relative to interspace-associated plants.

Finally, total individual fruit production (question d) increased with plant size ($F_{1,134} = 68.04$; $P < 0.001$) but was not influenced by microhabitat ($F_{1,134} = 0.19$; $P = 0.668$) or its interaction with plant size ($F_{1,134} = 0.11$; $P = 0.746$) (Fig. 2-6d).

Prediction 2d: To summarize, the performance metric being evaluated influenced the observed net effect of shrubs (positive, neutral, or negative) on *P. palmeri* (Table 2-4). The 2008 cohort of juveniles and adults at LC demonstrated associative interspecific spatial patterns with shrubs and higher survival under shrubs (positive effects), but when growth differences were detected, shrub-associated plants had lower growth rates and smaller sizes than did interspace-associated plants (a negative effect). In addition, relative to interspace-associated plants, shrub-associated plants had a lower likelihood of initiating reproduction when small plants were compared (negative effect) but had a higher bud-to-fruit maturation when larger plants were compared (positive effect). For the 2010 cohort, emerged seedlings demonstrated dissociative interspecific spatial patterns with shrubs, but survival was higher for shrub-associated seedlings compared to interspace-associated seedlings at LC and LKC (positive effect) and no survival differences were detected between microhabitats at MKC (neutral effect).

Prediction 2e: Plant size also influenced the observed effect of shrubs on survival and reproduction (Table 2-4). When size was significant, survival differences between shrub-associated and interspace-associated *P. palmeri* were greatest when small plants were compared,

Table 2-4

Comparison of the effect of shrubs on various metrics of *P. palmeri*. '+' indicates a positive effect of shrubs, '−' indicates a negative effect, '0' indicates a neutral effect ($P < 0.05$ unless noted otherwise), and '.' indicates unanalyzed comparisons. For spatial patterns, signs on the left and right of the '/' correspond to interspecific spatial patterns at the beginning and end of the study, respectively; further, '+' indicates associative patterns, '−' dissociative patterns, and '0' indicates patterns no different from random.

	LC site			**LKC site**			**MKC site**		
	Cohort			**Cohort**			**Cohort**		
Metric	**2008**	**2010**	**2011**	**2008**	**2010**	**2011**	**2008**	**2010**	**2011**
Spatial pattern w/ shrubs	+/+	−/0[1]	+/.	+/+	−/0[1]	0/.	+/+	−/0[1]	0/.
Survival	+[2]	+[2,3]	.	0[1]	+[2]	.	0[1]	0	.
Size at first census	0	+[3]	.	.	0		.	0	.
Growth (*RGR*)	0	.	.	.	.	.	.	.	.
Reproduction									
a) Likelihood of initiating reproduction	−[2]	.	.	.	.	.	.	.	.
b) Number of initiated buds	NS	.	.	.	.	.	.	.	.
c) Percentage of buds maturing to fruits	+[4]	.	.	.	.	.	.	.	.
d) Number of fruits matured	NS	.	.	.	.	.	.	.	.

[1] Analysis may be limited by sample size

[2] Estimated effect was most pronounced for smaller individuals

[3] Evidence was less compelling, but noteworthy; $0.05 < P < 0.100$

[4] Estimated effect was most pronounced for larger individuals

Note: Spatial pattern analyses did not include covariates for plant size

regardless of which cohort was examined. For reproduction models, microhabitat association had a stronger effect on the likelihood of initiating reproduction when *P. palmeri* were smaller, but microhabitat association had a stronger effect on the percentage of buds that matured when plants were larger.

V. Discussion

It is now recognized that positive and negative interactions occur simultaneously between plants (Callaway 1995, 2007 pp 179-256) and positive interactions should be stronger than negative interactions in stressful environments (Bertness and Callaway 1994), especially when comparing smaller plants (Callaway and Walker 1997) and plants of earlier ontogenetic stages (Miriti 2006). The results of this study add to this understanding by providing evidence that in this arid environment, shrubs facilitated the survival of the smallest and youngest *P. palmeri*, but as individuals developed, the balance between competition and facilitation became increasingly competitive. Further, examining spatial patterns over time provided evidence that facilitation of seedling survival drove the spatial patterning of *P. palmeri* toward being strongly associated with shrubs as interspace associated seedlings died. While shrub-association had important effects on survival, there was little evidence of growth difference between shrub and interspace microhabitats. However, there was evidence of complex effects of shrubs on *P. palmeri* reproduction, with shrubs negatively influencing the probability of initiating reproduction, but facilitating the successful maturation of buds into fruits. These results highlight the importance of providing a temporal description of spatial patterning (Lepš 1990) and examining multiple performance metrics over many life-stages and sizes when considering the balance of facilitation and competition (Callaway and Walker 1997; Miriti 2006; Schiffers and Tielborger 2006; Armas and Pugnaire 2009).

Objective 1: temporal descriptions of interspecific spatial patterns

Prediction 1a: Spatial patterns were predicted to be associative between *P. palmeri* and shrubs. Consistent associative interspecific spatial patterns among shrubs and the 2008 *P. palmeri* cohort of juveniles and adults supported the prediction, demonstrating that shrubs harbored higher than expected densities of *P. palmeri* beneath their canopies. Such patterns could indicate a history of facilitative interactions for this cohort, a notion that is supported by the evidence of facilitation of survival seen on the other, younger cohorts. However, interpreting associative ‘snapshot’ spatial patterns alone as evidence of historic facilitation is cautioned against (Lepš

1990; McIntire and Fajardo 2009); instead, interspecific spatial patterns should be described temporally alongside evidence of their effects on survival, growth, and reproduction and their utility should be limited to generating hypotheses that can later be tested manipulatively (Lepš 1990; McIntire and Fajardo 2009; e.g. Chapter 3).

In contrast, the dissociative patterns between the first cohort of emerged seedlings (2010) and shrubs, counter the prediction and suggest that relative to interspaces, shrubs may have inhibited *P. palmeri* seedling emergence. However, this conclusion should be considered cautiously since there were no measures of seed bank densities of *P. palmeri* in each microhabitat, making it impossible to know whether emerged seedling density was higher in interspaces because of higher emergence rates or due to higher seed-bank density. However, there is substantial evidence that persistent seed-banks form under shrub canopies, not their interspaces, (Pugnaire and Lázaro 2000) and a *P. palmeri* experiment at LKC controlling for seed-bank density demonstrated that seeds sown in sagebrush (*A. tridentata*) soil had lower emergence rates than those sown in interspaces (Chapter 3).

The second cohort of emerged seedlings (2011) had either associative (LC) or not different than random (LKC and MKC) spatial patterns with shrubs, partially supporting the prediction and suggesting that, relative to interspaces, shrubs at LC had higher seedling emergence densities of understory *P. palmeri* while at the other sites emergence was similar between microhabitats. Again, the lack of data on seed-bank densities challenges interpretation of this result; however, during the previous year, many seedlings emerged in the interspaces, which may have depleted the interspace seed-bank, while, in contrast, seeds may have persisted in shrub microhabitats until conditions were sufficient for germination and emergence. Unfortunately, without empirical evidence of seed-bank densities, this narrative should be considered with caution. Nonetheless, these results demonstrate the complexity of the study system and the variability of emergence patterns between years.

Prediction 1b: The existence and strength of associations between shrubs and *P. palmeri* were predicted to depend on shrub species identity. Interspecific spatial patterns between *P. palmeri* and shrubs varied with shrub species identity for all cohorts and sites (except for the 2008 cohort at LC) supporting the prediction and demonstrating the species-specific nature of spatial patterns (see Callaway 2007 pp 255–292). The drivers of these patterns remain unclear, but the results can be used to identify which species may be the most important facilitators of *P. palmeri* so that future studies can examine their interactions in more detail (e.g. Chapter 2 and Chapter 3).

Prediction 1c: *Penstemon palmeri* in interspaces were predicted to aggregate closer to shrubs than random points due to shrub effects potentially extending beyond their canopies. This prediction was not supported, suggesting that *P. palmeri* were distributed no different from random throughout the interspaces; such a pattern supports the hypothesis that interactions between shrubs and *P. palmeri* occurred under shrub canopies; processes like hydraulic lift (sensu Richards and Caldwell 1987) and shade extending past shrub canopies may not influence spatial patterns for interspace associated *P. palmeri*. Other studies have considered distance-dependence of plant interactions beyond canopies; for example, decreasing facilitative effects of hydraulic lift were found with increasing distance from trees (Dawson 1993) and in another study tree seedling growth and density were maximized at intermediate distance due to decreasing competition coupled with decreasing facilitation with increasing distance (Dickie et al. 2005); yet another study demonstrated that herbaceous biomass did not vary with distance from canopy edge, suggesting the tree interactions did not extend past tree canopies (Scholes and Archer 1997). However, these studies were different than this one in that they focused on trees rather than shrubs and provided performance based indicators of distance-dependent interactions rather than drawing inference from spatial patterning.

Prediction 1d: Interspecific spatial patterns were predicted to shift over time. As predicted, when cohorts were combined within sites, population-level interspecific spatial patterns shifted temporally (Fig. 2-3), highlighting the importance of temporally describing spatial patterns and demonstrating the complexity of the temporal component of spatial pattern. The shift from associative to dissociative patterns in 2010 was driven by higher than expected seedling emergence densities; this was followed by a shift in patterns back toward associative as mortality took place. Considering spatial associations only at the beginning of the study would have masked these fluctuations in spatial patterning and resulting in a gross oversimplification of spatial patterns. Others have observed similar complexities in spatial patterning over time (Rousset and Lepart 1999) and across climatic conditions (Tielbörger and Kadmon 2000), but I know of few examples where a temporal component was considered when evaluating spatial association (discussed in sub-section '*Prediction 2c*' below).

Objective 2: evaluation of plant performance

Prediction 2a: Survival was predicted to be higher for shrub-associated *P. palmeri*. Though survival differences between microhabitats were not always observed, when differences were detected, survival under shrubs was always higher than in interspaces and the estimated difference was always greatest for smaller plants, supporting the prediction and suggesting that shrubs facilitate survival of smaller individuals, but that as they grow, shrubs had less influence on survival; others have found similar shifting effects due to increased competition with beneficiary development (reviewed in Miriti 2006; Callaway 2007 pp 15–116; Gómez-Aparicio 2009). However, a decline in competition with beneficiary development has also been observed (Soliveres et al. 2010). Others have found higher survival among larger seedlings alongside evidence of facilitation of survival by shade during summer months, but they did not analyze the potential interaction between size and microhabitat in their analyses (Hastwell and Facelli 2003). Another study considered size and adult proximity as potentially important factors for seedling survival, however, while their survival analyses controlled for plant size, its statistical interaction with adult proximity was not assessed (Mulligan and Kirkman 2002).

Prediction 2b: Shrub species identity was predicted to influence *P. palmeri* survival. This was supported, but only for the 2008 cohorts at LC and LKC and the 2010 cohort at LC; for these sites and cohorts there was evidence that survival was higher for *P. palmeri* associated with certain shrub species relative to others (Table 2-3). These results add to the substantial evidence of species-specific effects of shrubs on survival of understory plants (Muller 1953; Callaway and D'Antonio 1991; Rudgers and Maron 2003; Landero and Valiente-Banuet 2010). Species specific effects could arise if certain benefactor traits facilitate *P. palmeri* survival more than others (see Callaway 2007 pp 255–292); e.g. N-fixation in *C. greggii* (Kummerow et al. 1978) and hydraulic lift in *A. tridentata* (Richards and Caldwell 1987). Dissimilar positive effects (e.g. canopies of some shrub species may have higher light transmission than others; Jones 1995) and/or differing negative effects (e.g. allelopathic leachates in the litter of some species but not others; Muller 1953) could both be responsible for species specific survival differences(reviewed in Callaway 2007 pp 255–292). It should be noted that survival was not always species specific, in part because too few *P. palmeri* grew under some potentially important shrub species, limiting inference due to small sample sizes. Also, no adjustments of *P*-values were made for pair-wise survival comparisons, increasing type I error; thus, some caution should be exercised in drawing strong conclusions from these results.

Prediction 2c: Higher survival of shrub-associated *P. palmeri* was expected to shift spatial patterns with shrubs toward associative. Comparisons of pre- and post-mortality interspecific spatial patterns between shrubs and *P. palmeri* supported this prediction at all sites cohorts analyzed, except for at MKC. At the remaining sites, spatial patterns either trended toward associative over time or remained strongly associative; this, in conjunction with the evidence of often higher survival under shrub canopies, suggests that shrubs facilitated *P. palmeri* survival, shifting spatial patterns between *P. palmeri* and shrubs toward being associative. The mechanisms driving survival differences are unclear from these results alone, however, experimental evidence suggests that at LKC, *A. tridentata* soil properties have stronger effects on *P. palmeri* seedlings than canopy related effects (Chapter 3). Many studies have used single observations of interspecific spatial patterns to generate and test predictions about survival (Turner et al. 1966; Callaway et al. 1996; Casper 1996; Greenlee and Callaway 1996; Tirado and Pugnaire 2003). However, other researchers have described a temporal shift in interspecific spatial patterns between *Quercus humilis* seedlings and shrubs; spatial patterns shifted from no different than random, before sheep grazing took place, to associative, after sheep grazing took place, providing strong evidence that shrubs facilitated *Q. humilis* seedling survival by protecting seedlings from predation (Rousset and Lepart 1999). Another study found a shift from either initially dissociative to no different than random, or from no different from random to associative, during years of higher precipitation which was interpreted as evidence that the negative effect of shrubs on density increased during dry years due to rainfall interception by canopies (Tielbörger and Kadmon 2000).

Size and growth: Of all the metrics compared, differences in size and growth among *P. palmeri* living in different microhabitats were the weakest; however, the analyses were severely limited due to high mortality rates and scarcity of *P. palmeri* in either interspaces (2008 cohort) or under shrub (2010 cohort). The most compelling evidence of size differences came from the 2010 cohort at LC, where shrub-associated *P. palmeri* appear to be slightly larger; however, the statistical support for this effect ($P = 0.074$), while suggestive, should not be considered conclusive, especially given that most observations came from a single plot at a single site. Weaker, but still noteworthy, evidence of size and growth differences came from the 2008 cohort at LC in which models estimated higher growth rates of interspace-associated *P. palmeri* surviving between the first and second census; however, while this evidence alludes to a competitive effect of shrubs on *P. palmeri* growth, the statistical support for this effect (P = 0.161) was merely suggestive. Failure to detect strong size and growth differences between microhabitats is partially a consequence of the limited sample sizes, however, they may also suggest neutral effects of shrub-association at later life-stages, despite the positive effects shrubs had on seedling and juvenile survival. This would suggest that shrubs facilitate smaller, younger individuals but not larger, older individuals, a commonly observed life-stage conflict (sensu Schupp 2007) in which interactions shift from facilitative toward competitive as the beneficiary develops (Miriti 2006; Gómez-Aparicio 2009). These apparent negative shifts in net-interactions with decreased abiotic stress are commonly reported as the outcome of simultaneously increasing competition with increased resource availability alongside a decreased benefit of ameliorated stress with less stressful conditions, however, experimental approaches are required to discern positive from negative effects (Callaway 2007 pp 15–116; e.g. Maestre et al. 2003).

Reproduction: The observed effect of shrubs on *P. palmeri* reproduction depended on which reproductive question (i.e. response) was being addressed and the size of *P. palmeri* (see Fig. 2-6b) supporting other studies showing that reproductive patterns depend on plant size (Bonser and Aarssen 2009; Weiner et al. 2009) and can differ between shrub-associated and interspace-associated plants (Casper 1996; Shumway 2000; Tielbörger and Kadmon 2000; Choler et al. 2001; Kikvidze et al. 2001; Tirado and Pugnaire 2003; Cranston et al. 2012). Some of these studies examined the effect of shrubs on reproductive initiation (Casper 1996; Shumway 2000; Choler et al. 2001) and/or seed or fruit production (Casper 1996; Tielbörger and Kadmon 2000; Kikvidze et al. 2001; Tirado and Pugnaire 2003) but none included size as a covariate for reproductive metrics (but see Soliveres et al. 2010) and none examined the fate of buds as they mature to fruits (but see Tirado and Pugnaire 2003 in which shrubs increased benefactors flower-to-fruit maturation). Though resource availability and abiotic conditions were never examined in this study, interspaces are often associated with highly variable abiotic conditions (Tracol et al.

2011) as well as limited resources (Noy-Meir 1985; Schlesinger et al. 1996; Maestre et al. 2003; Gómez-Aparicio et al. 2004; Cortina and Maestre 2005). Limited and unpredictable resources could explain the observation of high probability of initiating reproduction for interspace-associated plants relative to shrub-associated ones since plants often respond to these factors by investing in reproduction instead of growth; under these conditions, investing in growth may be 'unwise' since resources could be unavailable in the future resulting in mortality before reproduction (Stearns 1976; Reekie and Bazzaz 2005; Bonser and Aarssen 2009). In light of reproductive strategies, these results suggest that interspace-associated plants follow a strategy of early reproductive investment (an 'r-selected' strategy; sensu MacArthur and Wilson 1967), while shrub-associated plants follow a strategy of investing in growth before attempting reproduction (a 'K-selected' strategy; sensu MacArthur and Wilson 1967). For shrub-associated plants, a K-selected strategy may be more favorable than an r-selected strategy since shrub-associated plants had higher bud-to-fruit maturation rate when they were larger while interspace-associated plants saw no benefit in bud-to-fruit maturation rates from being large. A simpler and more likely explanation is that competition with shrubs or higher densities of conspecifics under shrubs may have limited the resources available to reproduction resulting in delayed reproduction of shrub-associated plants (Weiner 1988). While some authors have found a similar pattern of apparent delayed reproduction under shrubs (Casper 1996), others found the opposite (Shumway 2000; Choler et al. 2001). These contrasting results may be due to the latter studies being from sub-alpine systems rather than arid and semi-arid systems. Larger plants had higher total bud and fruit production suggesting that early reproduction has a consequence of lower fruit production; however, the advantages of early reproduction may outweigh the disadvantages when mortality is high, as it was in interspaces, since reproduction early with low output is better than dying before reproducing. Interestingly, despite these important reproductive differences between microhabitats, total bud initiation and fruit production was not significantly influenced by microhabitat suggesting that the effects of competition and facilitation on bud and fruit production were balanced under shrub canopies. Many studies of reproduction have observed increased output for plants aggregated with other species (Shumway 2000; Tielbörger and Kadmon 2000; Tirado and Pugnaire 2003), though this is not always the case; Soliveres et al. (2010) found that larger shrubs produced more fruits, but growing near grass tussocks had no effect on reproduction. The mechanisms responsible for differences in reproductive patterns between microhabitats remain unknown without experimental manipulation, but these results suggest that incorporating concepts of facilitation with well-studied topics like reproductive allocation strategies (Stearns 1976; Reekie and Bazzaz 2005) may lead to a more complete theoretical framework (e.g. Kikvidze et al. 2001; Cranston et al. 2012).

Prediction 2d: The observed effect shrubs had on *P. palmeri* depended on which performance metric was evaluated, supporting this prediction (see Table 2-4). While there was poor support for differences in growth rates, facilitation of survival coupled with reductions in growth rates is commonly reported (reviewed in Gómez-Aparicio 2009). However, few studies examine emergence, survival, growth, and reproduction in unison (but see Casper 1996 and Soliveres et al. 2010). Casper (1996) compared survival, growth, and flowering of the perennial forb *Cryptantha flava* and reported that shrub-associated *C. flava* had increased survival but reduced plant size, likelihood of flowering, and inflorescence production; emergence and bud-to-fruit maturation rates were not considered in the study. Flowering and survival were probably limited by different environmental factors, with shade perhaps decreasing water loss in seedlings, improving their survival, but shade also limiting photosynthesis, reducing growth and flowering (Casper 1996). Soliveres et al. (2010) provided experimental evidence that associative spatial patterns between a grass (benefactor) and a shrub (beneficiary) were primarily determined during the seed stage by higher than expected shrub seedling emergence in grass tussocks, but that growth of grass-associated shrub seedlings was limited; however, in their study, high mortality was associated with drought for all shrubs and precluded survival analysis and fruit production depended only on plant size.

The combined interspecific spatial patterns and survival analyses from the 2010 cohort suggest a seed-seedling conflict (Schupp 1995); initially dissociation between shrubs and *P. palmeri* emerged seedlings may indicate reduced emergence under shrubs, a negative effect on the seed stage, but survival was subsequently improved at the seedling stage; these types of seed-seedling conflicts appear to be widespread (Schupp 1995). For example, an experimental study determined that litter of *Cercocarpus ledifolius* inhibited emergence, but improved survival of seedlings of the tree *C. ledifolius* (Ibáñez and Schupp 2002). In another study at LKC emergence of seedlings from sown-seeds was higher in shrub soils than interspace soils, but their subsequent survival was lower, a pattern matching the natural patterns observed here; further, experimental manipulations (shrub removal and canopy mimicry) demonstrated that seedling emergence was better explained by association with *A. tridentata* soil than by canopy presence or absence, suggesting soil properties may be very important determinants of seed-seedling conflicts in *P. palmeri* (Chapter 3).

Prediction 2e: As expected, size was an important factor to consider when evaluating survival and reproduction (summarized in Table 2-4), yet few studies of facilitation include control over size (but see Mulligan and Kirkman 2002; Hastwell and Facelli 2003; Soliveres et al. 2010) despite its predicted importance in influence the outcome of interactions (Callaway and Walker 1997). Studies considering size, microhabitat, and their interaction in a single analysis were not found when reviewing literature, however, by their inclusion as covariates added insight into the size-dependence of the balance between facilitation and competition.

Conclusion

This study revealed that shrubs can be of great importance for the spatial distribution, emergence, survival, and reproduction of *P. palmeri*. The precise demographic and fitness impacts of shrubs on *P. palmeri* remain unclear since little is known about seed survival and total life-time reproductive output in contrasting microhabitats; however, these observations demonstrated that shrub-association can have complex and conflicting demographic effects at different life-stages, increasing performance of some life-stages and decreasing performance of others. By temporally observing interspecific spatial patterns alongside emergence and survival, insight was gained regarding the role of emergence and survival differences between shrub and interspace microhabitat in driving the spatial patterning of *P. palmeri* populations. These results add to a growing body of evidence of ontogenetic shifts in plant-plant interactions throughout the life-cycle of an organism (e.g. Miriti 2006; Armas and Pugnaire 2009; Gómez-Aparicio 2009; Soliveres et al. 2010) and suggest that shrubs potentially alter the nature of life-stage conflicts in a way that could promote persistence of *P. palmeri* populations during unfavorable conditions.

VI. References

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CHAPTER 3

DISENTANGLING CANOPY AND SOIL EFFECTS OF A COMMON DESERT SHRUB ON A PATCHILY DISTRIBUTED PERENNIAL HERB IN THE MOJAVE DESERT

I. Abstract

In water-limited ecosystems, microhabitat conditions under shrub canopies often contrast the conditions in interspaces. For example, sub-canopy shade and ‘fertile islands’ can provide more habitable conditions than interspaces exposed to direct insolation and with relatively denuded soils. Seeds and seedlings respond to these distinct microhabitats in complex and potentially conflicting ways. I experimentally examined the relative importance of *Artemisia tridentata* (Nutt.) canopy presence or absence versus soil microhabitat (shrub vs. interspace) and their potentially interacting effects on seedling emergence, survival, size, and growth of the herbaceous perennial *Penstemon palmeri* (A. Gray). I sowed *P. palmeri* seeds and transplanted greenhouse-reared seedlings into four microhabitats: (1) no canopy with interspace soil, (2) canopy with shrub soil, (3) canopy with interspace soil, or (4) no canopy with shrub soil. In both experiments, relative to soil microhabitat, canopy presence had little effect on emergence and seedling performance. Further, when the net effects of canopies were detected, they depended on soil microhabitat. Shrub soils had lower emergence but higher seedling survival relative to interspace soils in the seed-sowing experiment; seedlings emerging on shrub soils had higher survival in the presence of canopy shelter, but canopy presence had no effect on emerged seedling survival in interspace soils. In contrast to emerged seedling survival, transplanted seedling survival was lower on shrub soils and canopies had no effect. Shrub soils had a positive effect on transplanted seedling size and growth in the absence of canopies but canopy presence decreased seedling size and growth on shrub, but not interspace, soil. The response of *P. palmeri* depended

largely on soil microhabitat and the plant response and experiment being considered. Results of the seed sowing and seedling transplant experiments conflicted, but both suggest soil microhabitat had a greater effect on survival regardless of canopy presence or absence. Both experiments also demonstrated that canopy effects depended on soil microhabitat. Finally, the demographic consequences of these results are considered: shrub soils appeared to alter seed-seedling conflicts in a way that might promote seed bank persistence and therefore resistance and resilience of *P. palmeri* populations to environmental perturbations.

II. Introduction

The topic of facilitation has received substantial attention in ecology (Brooker et al. 2008; Brooker and Callaway 2009). Facilitation and interference act simultaneously to determine the net interactions between plants; their balance varies spatially, as along productivity gradients (Brooker et al. 2008), and temporally due to progressive development of interacting plants and climatic variability (Kitzberger et al. 2000; Tielbörger and Kadmon 2000; Miriti 2006; Armas and Pugnaire 2009; Gómez-Aparicio 2009). Community dynamics in arid environments are thought to be dominated by positive net plant-plant interactions (Pugnaire et al. 1996; Callaway and Walker 1997). Shrubs frequently facilitate the performance of other species beneath their canopies (Callaway 1995; Gómez-Aparicio 2009; Reisner 2010) (i.e., are benefactors, sensu Callaway 1995) and can increase the persistence of seeds in the seed bank (Pugnaire and Lázaro 2000). For desert plants, water is limited, variable, and unpredictable and persistent seed banks allow plant populations to remain dormant until precipitation events are large enough to trigger a pulse of germination (Noy-Meir 1973; Reynolds et al. 2004).

In water-limited systems, relative to shrub canopy microhabitat, the shrub interspaces are often characterized by extreme temperatures and insolation (Tracol et al. 2011) and limited resource availability (Garcia-Moya and McKell 1970; Schlesinger et al. 1996; Gómez-Aparicio et al. 2005; van der Heijden and Horton 2009; Bashan and de-Bashan 2010), conditions that can inhibit germination and be physiologically stressful for seedlings (Aro et al. 1993; Callaway pp 15-116; Murata et al. 2007; Lambers et al. 2008). Shrubs can ameliorate stressful interspace conditions by altering local microhabitat via an above-ground 'canopy effect,' a below-ground 'soil effect,' and their interacting effects (Callaway 1992, 2007 pp 15-116; Carrillo-Garcia et al. 2000; Gómez-Aparicio et al. 2005; Becerra and Bustamante 2011).

Canopy effects on emergence and survival are complex, acting directly and indirectly through alterations of the physical, chemical, and biotic conditions (Facelli and Picket 1991; Callaway 2007 pp 15-178). Physical shelter of the shrub canopy can influence seeds and seedlings through direct effects of shade, which can have positive effects on understory seedlings if water is limited (Kitzberger et al. 2000; Maestre et al. 2003; Gómez-Aparicio et al. 2005; Callaway 2007 pp 15-116). However, the negative effects of shade may increase as seedlings develop, resulting in reduced survival and growth under shaded conditions (Kitzberger et al. 2000; Miriti 2006; Armas and Pugnaire 2009; Gómez-Aparicio 2009). Further, interactions between canopy shade and soil microhabitat can improve plant performance under canopies. Canopy shade can directly reduce air and soil temperatures, thereby reducing evaporation of water in soils and increasing root and microbial activity (Kitzberger et al. 2000; Shumway 2000; Gómez-Aparicio et al. 2005; Becerra and Bustamante 2011). Further, indirect effects of canopies can arise when the physical structure of canopies alters the foraging intensity of seed and seedling predators as through 'associational resistance and 'associational susceptibility' (sensu Barbosa et al. 2009). Associational resistance may occur when the canopy prevents access to, or obscures, understory seeds and seedlings from their predators (Callaway 2007 pp 117-178). Associational susceptibility may occur when the canopy protects seed and seedling consumers from their predators, leading to an indirect increased seed and seedling predation under canopies (Callaway 1992; Castro et al. 1999; Hulme and Borelli 1999; Vander Wall and Thayer 2001).

Unlike interspace soils, soils beneath canopies soils may effect litter input and buffer temperature and may also have differences in deeper soil profiles due to root related effects (Callaway 2007 pp 15-116). The physical, chemical, and biotic soil characteristics that are important for emergence and seedling performance are greatly impacted by the litter produced by canopies (Facelli and Picket 1991; Facelli 1994; Ibáñez and Schupp 2002). Sub-canopy 'Islands of fertility' (sensu Schlesinger et al. 1996) form due to litter inputs, throughfall, and microbial activity (Garcia-Moya and McKell 1970; Schlesinger et al. 1996; van der Heijden and Horton 2009; Bashan and de-Bashan 2010). While litter can positively alter the environment faced by seeds and seedlings it also has potential negative effects on them as well; for example, seedling emergence and survival can be limited by high concentrations of phytotoxins in litter or lower water availability while emergence be further limited due to seeds being shaded by litter and/or litter forming a physical barrier for emerging seedlings (Facelli and Picket 1991; Facelli 1994; Ibáñez and Schupp 2002). Further, emerged seedling density can be low in litter since seeds can become buried and remain where light, temperature, and/or moisture conditions may be insufficient for germination (Kitchen and Meyer 1992; Pugnaire and Lázaro 2000). Litter can interact with canopy shade to further indirectly influence seedling performance by altering the temperature of soils through an albedo effect (Turner et al. 1966; Carrillo-Garcia et al. 2000). While these canopy effects on soils are important, the roots of shrubs can also influence deep water profiles via hydraulic redistribution (Ryel 2004), potentially altering surface water availability and the performance of other plants (Dawson 1993). Further, understory plants may respond to alterations of the rhizosphere by shrubs via root competition, nitrogen fixation, or exudation of water, nutrients, and allelopathic compounds (Callaway 2007 pp 15-116).

Alterations of microhabitat conditions by shrubs can influence seeds and seedlings in conflicting ways; conditions that are favorable for seedling emergence may later be unfavorable for seedlings (i.e. a "seed-seedling conflict" Schupp 1995). For example, litter under canopies can negatively affect seedling emergence but positively affect the survival of emerged seedlings (Ibáñez and Schupp 2002). In contrast, interspaces may have positive effects on the seed stage if interspace conditions promote emergence (e.g. warmer temperatures, or lack of competition for light and water) but have negative effects on seedlings if those conditions are unfavorable for growth or survival (e.g. Facelli and Ladd 1996). Thus, the stages of the seed-seedling conflicts that are improved or worsened may differ between interspace and shrub microhabitats.

Understanding the interacting effects of canopies and soils on emergence and survival requires manipulative experiments which, when combined with long-term patterns of spatial associations, can better distinguish the underlying mechanisms that drive the balance between positive and negative interactions (Lepš 1990; Callaway 1995, 2007 pp 255-292; McIntire and Fajardo 2009). Many studies use canopy removal to evaluate if shrubs act as benefactors to understory plants (e.g. Callaway 1992; Callaway et al. 1996; Holzapfel and Mahall 1999). Decreased understory plant performance in the absence of canopies suggests that shrubs act as benefactors while increased understory plant performance following canopy removal suggests that shrubs act as competitors (Callaway 2007 pp 15-116). However, canopy removal does not consider potential facilitation by modified soils beneath shrubs (Callaway 2007 pp 15-116) which can last many years after canopy removal (Bechtold and Inouye 2007); such lagged effects can lead to observations of neutral or even improved plant performance following shrub removal even if the canopy effect is positive (Callaway 2007 pp 15-116). Another manipulation for disentangling canopy and soil effects is the use of canopy-mimicry experiments, which use either shade cloth or mimic shrubs to simulate the shade and shelter conditions of a shrub canopy without the effects of accumulated soil under canopies (Holzapfel and Mahall 1999; Callaway 2007 pp 15-116; Padilla and Pugnaire 2008). While canopy mimicry experiments allow for explicit comparisons of the effect of shade on plants living in interspace soils, they cannot account for the effect of shade when plants live in shrub soils; similarly, canopy removal experiments provide no information on the effect of shade when plants live in interspace soils. The importance of the potentially interacting effects of shrub canopies and their associated soils on seedling emergence and performance can be evaluated better in field conditions using a factorial combination of removal and shrub-mimic manipulations (see Gómez-Aparicio et al. 2005).

Natural observation of spatial association at the experimental site during this study suggested that emerging seedlings of the perennial forb *Penstemon palmeri* were negatively associated with shrubs, including *Artemisia tridentata*; that is, seedlings emerged in interspaces more frequently than expected by chance. This pattern may be caused by greater emergence rates in interspaces relative to beneath shrubs suggesting a net negative effect of shrubs on emergence (Chapter 2). However, high seedling and adult mortality in interspaces disproportionately decreased densities, promoting positive spatial associations between shrubs and *P. palmeri* over time; i.e., surviving plants were found beneath shrubs increasingly more often than expected by chance (Chapter 2). These results suggested a seed-seedling conflict in which shrubs negatively influenced the seed emergence stage but positively influenced the seedling survival stage. However, without experimental manipulations as described above, determination of the mechanisms responsible for these patterns is impossible.

The objectives of this study were to experimentally determine the relative importance of two broadly defined and interacting shrub microhabitat effects, canopy cover and soil microhabitat, for *P. palmeri* (1) emergence from sown seeds and (2) performance (i.e. size, growth, and survival) of seedlings recruited from sown seeds and transplanted seedlings. I compared these experimental results to natural patterns of spatial associations (Chapter 2) and discuss the implications for the population dynamics of *P. palmeri*.

III. Materials and Methods

Study site

The study was conducted in a Mojave Desert shrubland in the Spring Mountains National Recreation Area (SMNRA), an isolated mountain range (‘Sky Island’) within the Mojave Desert of southern Nevada, USA (approximately 50 km northwest of downtown Las Vegas). Experimental units were established in a shallowly sloping (slope <5°) wash in Lower Kyle Canyon (Lat.: 36° 16' 18.867" N, Long.: 115° 31' 17.328" W; Elevation: 1626 m – 1677 m). Climate data for the maximum temperature, minimum temperature, and precipitation were obtained from the years 2000 - 2010 (PRISM Climate Group). For the first and second years of the study (2009-2010) mean annual precipitation (MAP) was about 25% higher and 68% lower than the 2000-2008 mean, respectively ($MAP_{2000\text{-}2008}$ = 360 mm; MAP_{2009} = 451 mm; MAP_{2010} = 221 mm). Temperatures in both 2009 and 2010 were similar to the mean (MAT_{2009} = 12.4°C; MAT_{2010} = 12.6°C; $MAT_{2000\text{-}2008}$ = 12.4°C). Peak precipitation occurs during winter (November–March) with a pronounced dry season (April–mid-July) followed by varying intensities of monsoons (mid-July – September) and intermediate precipitation (September–November). In 2009 and 2010, respective winter precipitation (WP) was 41% and 55% higher than the 2000-2008 mean ($WP_{2000\text{-}2008}$= 204 mm; WP_{2009} = 288 mm; WP_{2010} = 317 mm) and monsoon precipitation (MP) was roughly 13% (2009) and 73% (2010) less than the 2000-2008 mean ($MP_{2000\text{-}2008}$= 85 mm; MP_{2009} = 74 mm; MP_{2010} = 23 mm). Soils are purob-irongold associated; well-drained soils with a surface covered with cobbles and stones, a deep (>2 m) water table, and a shallow (25-35 cm) petrocalcic layer (Soil Survey Staff, NRCS USDA, 2011). Line point intercept estimates indicated that shrub cover was roughly 53% consisting of at least 11 shrub species (Chapter 2, Fig. 2-1, middle panel). At this site, *P. palmeri* grew under many shrub species more than expected based on the cover of all shrub species, but particularly *A. tridentata*

(Chapter 2, Fig. 2-1, middle panel). All plant names follow the USDA NRCS PLANTS database (NRCS 2011).

Penstemon palmeri commonly occurs in disturbed sites such as washes and roadsides throughout the arid south-western United States between 800 and 2500 m in elevation (Cronquist et al. 1984). It is considered to be drought and winter tolerant (USDA NRCS 2011). Seed banks can become persistent if seeds are buried in litter in part because breaking dormancy requires light if temperatures are below 30° C (Kitchen and Meyer 1992). Other evidence (Meyer and Kitchen 1992) suggests that most seeds are non-dormant at maturation, but rarely germinate in fall conditions, probably because they require sufficient periods of moisture to germinate. Seeds generally germinate in response to post-chilling conditions during early spring. *Penstemon palmeri* seeds vary in their response to variation in abiotic conditions, allowing them to persist in a dormant state until conditions are suitable to break dormancy (Meyer and Kitchen 1992).

Artemisia tridentata possesses several physiological and morphological characteristics that can positively or negatively affect understory species. In addition to providing shade, it was the first species used to demonstrate the existence of hydraulic lift (sensu Richards and Caldwell 1987), by which plant roots move water from deeper, wetter, strata to upper, dryer, strata of the soil profile (see Ryel 2004 for review). Lifted water can become available to shallow rooted plants (Dawson 1993), like forbs and grasses. It is unclear whether canopy removal results in a complete cessation of hydraulic lift because water is thought to move passively through roots (Ryel 2004). In addition, long-term soil fertility can be improved by *A. tridentata* even after removal due to an accumulation of nutrient-rich litter (Bechtold and Inouye 2007). These traits may help explain why *A. tridentata* frequently acts as a benefactor to herbaceous plants under stressful conditions in its northern range (e.g., Reisner 2010). However, allelopathic effects of *A. tridentata* litter and soil on plant performance are also widely documented (Schlatterer and Tisdale 1969; Weaver and Klarich 1977; Kelsey et al. 1978).

Seed Sowing

In mid-March 2009, *P. palmeri* seeds were sown into four experimental microhabitats (treatments) and their emergence and subsequent survival in the field were monitored. Treatments (i.e. microhabitats) formed a 2 x 2 fully factorial design consisting of a two-level soil factor (shrub soil vs. interspace soil) and a two-level canopy factor (canopy vs. no canopy). Two microhabitats occurred naturally: no canopy with interspace soil (NC+IS; i.e. natural interspaces) and canopy with shrub soil (C+SS; i.e. natural shrubs). The other two microhabitats were experimentally created; the no canopy with shrub soils (NC+SS; i.e. artificially exposed shrub soils) microhabitat was created by removing *A. tridentata* canopies. Canopy mimics were then created by spraying removed canopies with lacquer (for longer leaf retention; Callaway et al. 1996), and relocating them to interspaces to create the microhabitat for canopy with interspace soil (C+IS; i.e. artificially-sheltered interspaces). Soils surfaces were not disturbed. Each treatment combination was replicated 25 times and replicates were spaced every 20 m along 5 non-overlapping 100 m transects, excluding zero. Each replicate contained one of each of the four microhabitat types. Seeds of *P. palmeri* (200) were collected from 25 plants at the site and were mixed to form packets of 50 seeds per treatment. These packets were then sown on the surface of 20cm x 20cm “plots” for each treatment (Total seeds sown = 5000; 50 seeds per treatment × 4 treatments per replicate × 25 replicates); plots were spaced at least 5 m apart. When treatments involved canopies, seedlings were transplanted on the shady north side of canopies that were matched for similarity of size (~1 m diameter). Seedling emergence and subsequent survival were observed during 10 unequally spaced censuses over 528 days (14 April 2009- 29 September 2010). To estimate density of background *P. palmeri* seedling emergence, an adjacent 20cm x 20cm control plot was randomly assigned to either the east or west of the sowing plot and background emergence tallied.

Seedling Transplants

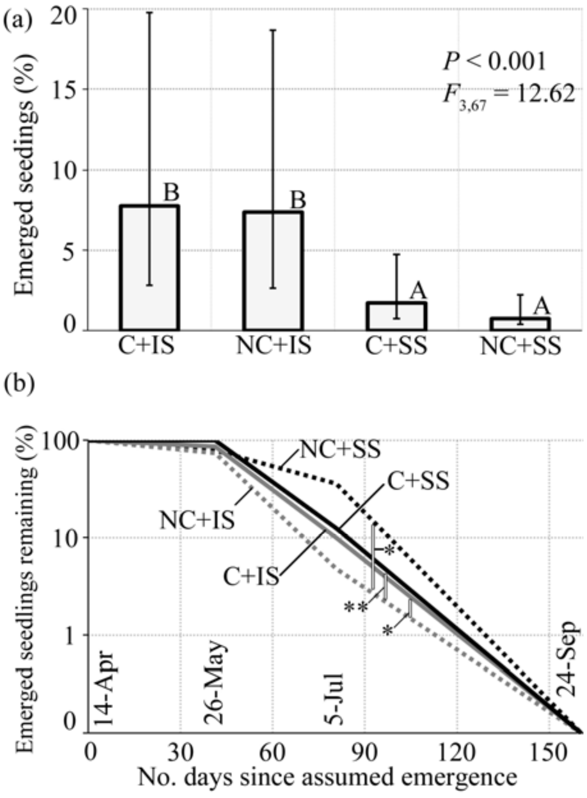
Seeds were collected from 25 *P. palmeri* individuals surrounding the study site, germinated, and grown in a sterilized 3:1 mixture of sand to Canadian peat moss, repectively, at the Research Greenhouses at Utah State University in Logan, UT, 6 months prior to transplanting; 45 days prior to transplanting (2 March 2009), seedlings were placed outside of the greenhouse to allow them to acclimate to aridity and increased fluctuations and extremes in temperature. In mid-April 2009, the same four microhabitats were again created by varying canopy presence or absence on either shrub or interspace soil. This experiment was replicated 21 times and replicates, representing each of the four microhabitats, were placed using the same transect methods described in the seed-sowing experiment. Plots were formed by transplanting nine seedlings into a 3 x 3 grid with 10 cm between adjacent seedlings forming a 20 cm x 20 cm plot. For each of 21 replicates, plots were established within each of the four microhabitats (15 April 2009), spaced at least 5 m apart. Seedlings were transplanted on the north side of similarly sized (~1 m diameter) canopies. The 21 replicates resulted in 189 seedlings per microhabitat and 756 seedlings total (nine seedlings per treatment × four treatments per replicate × 21 replicates). To mediate transplant shock (sensu Close et al. 2005), plants were watered weekly, starting with 3.78 liters per plot and ending with about 0.5 liters per plot at day 126 (decreasing by approximately 0.2 liters per week); ample time was taken to ensure that water infiltrated into the soil rather than running off. Growth and survival were monitored as in the seed sowing experiment described above. To estimate aboveground volume (*AGV*), measurements of the major diameter, its perpendicular diameter, and the height of above-ground living tissue for each seedling were taken and used to parameterize the equation for an ellipsoid ($AGV = \frac{\pi abc}{6}$, where a is the major diameter, b is its perpendicular diameter and c is plant height). Size and growth were only assessed for seedling transplants since sample sizes in the seed sowing experiment were limited.

Every canopy mimic in the seedling transplant experiment remained sturdy, but five canopy mimics in the seed sowing experiment blew over due to strong winds (these plots were excluded from analyses). For both experiments, leaves on canopy mimics remained mostly intact until day 126 (18 August 2009), but by day 203 (3 November 2009) most leaves had fallen off. While the size measurements in the seedling transplant experiment all occurred before this and >90% of mortality had already taken place in all treatments, emergence in the seed sowing experiment was not observed until 407 days after canopy mimics were installed; the implications of this are that canopy mimics eventually provided less shade than natural canopies, but the entire woody portion of the canopy remained, still offering some shelter and shade.

Analyses

Seed Sowing: Differences in emergence between treatments were modeled using generalized linear mixed models (GLMMs) with the GLIMMIX prodecure in SAS 9.2 (SAS Institute Inc. 2008). A binomial distribution was assumed for the response (number of emerged seedlings [successes] ÷ number of seeds sown [trials]). To account for possible non-independence of plots within replicates, random effects were assigned to replicates; an overdispersion parameter was also included. Tukey-Kramer adjustments were used to assess significance for pair-wise comparisons between treatments. Individual seedling survival was analyzed using Cox proportional hazard (PH) regression models with the PHREG procure in SAS 9.2 (SAS Institute Inc. 2008), which estimates each individuals ‘hazard’, or risk of death, in response to the covariates associated with a given individual, e.g. microhabitat. Two additional options were used within the PHREG procedure: (1) the COVSANDWICH option to estimate robust Wald sandwich covariance (Lee et al. 1992) since individuals are non-independently clustered as plots within replicates, and (2) the EXACT ties option, which should be used when the true timing of mortality is unknown and could occur during any continuous point between censuses (Allison 2010). Interpreting Cox PH models is fairly intuitive since a Hazard Ratio (HR) for each covariate is produced. For categorical variables, the HR quantifies the hazard for one group (numerator) relative to another (denominator); e.g. the hazard associated with growing beneath shrubs relative to interspaces. Size was not used in survival analyses of seedlings emerged from sown seeds.

IV. Results



* $P < 0.05$; ** $P < 0.01$

Fig. 3-1: (a) The percentage of seeds that emerged as seedlings in each microhabitat and results of a generalized linear mixed model showing the associated 95% confidence limits. (b) The proportion of seedlings that survived in each microhabitat over time. Significance tests result from Cox PH modeling and indicate significance between pair-wise comparisons of hazard ratios (see Table 3-2).

Seed-sowing experiment

Emergence occurred between the censuses of 4 November 2009 and 28 May 2010, probably in April or early May, since most seedlings only had cotyledon leaves. When first observed in May, the desiccated remains of dead seedlings included in emergence and survival analyses. Seedling emergence was never observed in control plots of any treatment suggesting all seedlings were from the seeds I had sown.

Emergence was significantly influenced by microhabitat association (Fig. 3-1a). Pair-wise comparisons indicate canopy presence (C) or absence (NC) had no effect on emergence (Table 3-1; Fig. 3-

Table 3-1

Pair-wise comparisons of emergence between treatments resulting from the GLMM using the GLIMMIX procedure in SAS 9.2 (SAS Insititute Inc. 2008). Tukey-Kramer significant adjustments are reported (P_{adj}). Emergence occurred either under a canopy (C) or no canopy (NC) in either shrub soil (SS) or interspace soil (IS). To account for potential non-independence within replicates, G-sided random effects were specified at the replicate level. Bolding indicates significance at the 0.05 level. The overall model was significant ($P < 0.001$; $F_{3,67} = 12.62$)

Microhabitat comparisons			Estimate	SE	T_{67}	P_{adj}
C+ SS	**vs.**	**C+IS**	**-1.595**	**0.375**	**4.22**	**<0.001**
C+ SS	vs.	NC+SS	0.848	0.589	1.44	0.478
C+ SS	**vs.**	**NC+IS**	**-1.477**	**0.371**	**3.98**	**0.001**
C+IS	**vs.**	**NC+SS**	**2.434**	**0.523**	**4.66**	**<0.001**
C+IS	vs.	NC+IS	0.109	0.254	0.43	0.974
NC+IS	**vs.**	**NC+SS**	**2.325**	**0.520**	**4.47**	**<0.001**

1a). In contrast, emergence was more than 4.7 times greater in interspace soils relative to shrub soils, regardless of shrub canopy presence or absence (Table 3-1, Fig. 3-1a).

Hazard (ie. risk of mortality) of emerged seedlings was influenced by microhabitat (Table 3-2a; Fig. 3-1b). Pair-wise hazard comparisons between microhabitats revealed that seedlings emerging in natural interspaces (NC+IS) had 32%, 45%, and 65%, higher hazard than the C+IS, C+SS, and NC+SS treatments, respectively, but all other treatments were indistinguishable (Table 3-2a; Fig. 3-1b). Summarizing in other words, seedlings growing in shrub soil had higher survival regardless of canopy presence, but survival of seedlings was only greater under canopies if seedlings emerged from interspace soils. Although these differences in initial survival rates are enlightening, all seedlings died before becoming reproductive.

Seedling-transplant experiment

Initial size (*AGV*) of transplants did not differ significantly between microhabitats (Table 3-3). To avoid interpreting size-dependent mortality as growth, I only compared size and growth for transplants surviving to day 77; too few plants survived past day 77 for reliable growth analyses (Fig. 3-2). This limited the number of transplants used for size and growth analyses in each microhabitat to 25 (C+SS), 75 (C+IS), 27 (NC+SS), and 59 (NC+IS).

Table 3-2

Pair-wise microhabitat comparisons of hazard ratios (HR) and their 95% confidence limits (CL), goodness of fit (Wald $\chi^2_{df=1}$) and statistical significance for (a) seedlings emerged from seed and (b) average sized transplanted seedlings of *P.palmeri*. Seedlings grew either under a canopy (C) or no canopy (NC) in either shrub soil (SS) or interspace soil (IS). All comparisons result from Cox PH models using SAS 9.2 (SAS Institute Inc. 2008) with EXACT ties (Allison 2010). Non-independence was accounted for using robust Wald sandwich covariance's (Lin and Yei 1992) using the COVSANDWICH option at the subplot (20cm x 20cm) scale. Bolding indicates significance at the 0.05 level.

(a) *Emerged seedlings* [a]

Microhabitat Comparison			HR[c]	Wald 95% CL	Wald χ^2_1	*P*-value
C+SS	÷	C+IS	0.808	0.565-1.154	1.378	0.241
C+SS	÷	NC+SS	1.563	0.688-3.550	1.137	0.286
C+SS	÷	**NC+IS**	**0.545**	**0.361-0.822**	**8.365**	**0.004**
C+IS	÷	NC+SS	1.935	0.869-4.311	2.609	0.106
C+IS	÷	**NC+IS**	**0.675**	**0.456-0.999**	**3.856**	**0.049**
NC+SS	÷	**NC+IS**	**0.349**	**0.150-0.813**	**5.954**	**0.015**

(b) *Transplanted seedlings* [b]

Microhabitat Comparison			HR[c]	Wald 95% CL	Wald χ^2_1	*P*-value
C+SS	÷	**C+IS**	**1.573**	**1.207-2.050**	**11.227**	**< 0.001**
C+SS	÷	NC+SS	1.043	0.839-1.297	0.146	0.702
C+SS	÷	**NC+IS**	**1.313**	**1.030-1.674**	**4.852**	**0.028**
C+IS	÷	**NC+SS**	**0.663**	**0.523-0.842**	**11.386**	**<0.001**
C+IS	÷	NC+IS	0.835	0.645-1.080	1.886	0.170
NC+SS	÷	**NC+IS**	**1.259**	**1.017-1.558**	**4.473**	**0.034**

[a] Overall the model/microhabitat effect were statistically significant ($P = 0.011$;$\chi^2_3 = 11.05$).

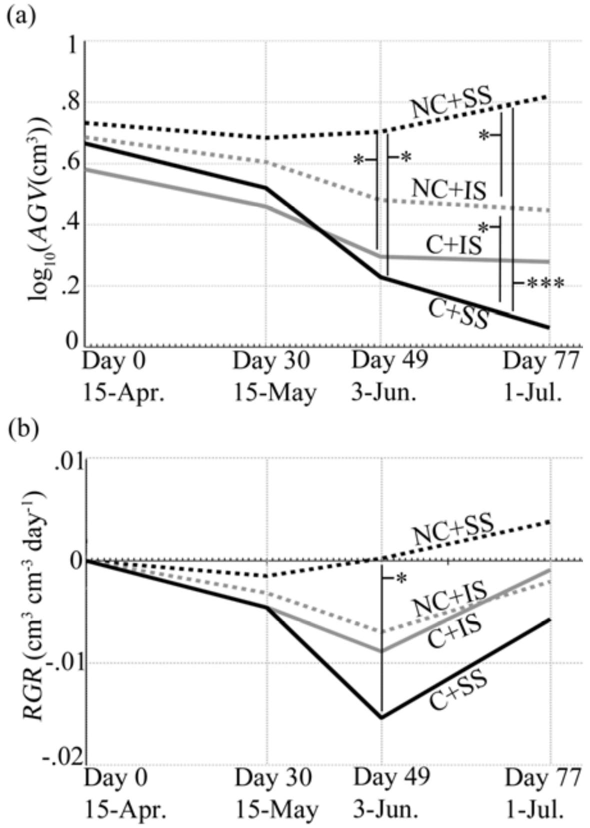
[b] The overall model fit was significant ($P < 0.001$; $\chi^2_4 = 79.138$) and included a statistically significant effect of Log_{10}[Initial transplant volume]($P < 0.001$; $\chi^2_1 = 65.151$; HR = 0.615). The microhabitat effect was statistically significant ($P = 0.001$; $\chi^2_3 = 16.08$). The interaction between microhabitat and plant size was not significant ($P = 0.230$; $\chi^2_3 = 4.039$), and was removed from the model.

[c] HR: 'Hazard Ratio'; the risk of mortality in the microhabitat in the numerator relative to the denominator.

Table 3-3

Summary of generalize linear mixed models for initial above ground volume (*AGV*), *AGV* over time, and relative growth rate (*RGR*) for transplanted *P. palmeri.* All models were evaluated using the GLIMMIX procedure in SAS 9.2 (SAS Institute Inc. 2008).

	Initial *AGV*			*AGV over time*			*RGR*		
Covariates	*F*	df	*P*-value	*F*	df	*P*-value	*F*	df	*P*-value
Microhabitat	0.20	3,60	0.895	4.20	3,56	0.009	4.92	3,48	0.005
Days	-	-	-	12.74	3,152	< 0.001	3.35	3,106	0.039
Microhabitat × days	-	-	-	2.91	9,152	0.003	0.45	6,106	0.842



* $P < 0.05$; *** $P < 0.001$

Fig. 3-2: Comparisons of (a) size ($\log_{10}$(*AGV*)) and (b) growth rate (*RGR)* of transplanted seedlings; significance was evaluated using Tukey-Kramer adjusted pair-wise comparisons of microhabitats based on generalized linear mixed models.

Above ground volume (*AGV*) was significantly influenced by microhabitat, the number of days since transplant, and their interaction (Table 3-3). Pair-wise comparisons show that there were no significant *AGV* differences between transplants in any microhabitat until day 49 (Table 3-4); after this, *AGV* was greater for transplants in the NC+SS microhabitat than in the C+SS and C+IS microhabitats (Fig. 3-2a; Table 3-4a). By day 77 these differences were amplified since transplants in NC+SS microhabitat continually increased in *AGV* after day 49 while those in the remaining microhabitats continued to shrink(Fig. 3-2a; Table 3-4a); however, the decrease in size was less for transplants in natural interspaces (NC+IS) compared to those beneath natural shrubs (C+SS) resulting in a significantly higher transplant *AGV* in the natural interspaces relative to the natural shrubs (NC+IS ÷ C+SS; Fig. 3-2a; Table 3-4a). The remaining microhabitat comparisons of transplanted seedling *AGV* were not statistically significant (Table 3-4a).

Transplant growth (*RGR*) was significantly influenced by treatment and the number of days since transplant but, unlike the model for *AGV*, not their interaction (Table 3-3). Pair-wise

Table 3-4

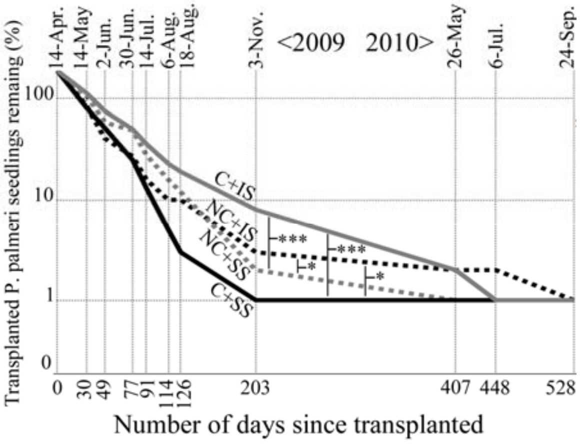
Statistical significance and parameter estimates for (a) size volume ($\log_{10}(AGV)$) and (b) growth (*RGR*) for transplants growing either under a shrub canopy (C) or no canopy (NC) in either shrub soil (SS) or interspace soil (IS). All analyses were conducted with GLMMs using the GLIMMIX procedure in SAS 9.2 (SAS Institute Inc. 2008) with G-sided random effects to account for non-independence within plots and R-sided effects to account for repeated measures. *AGV* was Log_{10} distributed and *RGR* was normally distributed. Bolding indicates significance at the 0.05 level. Tukey-Kramer adjusted significance of tests are reported to account for the inflation of Type I error due to multiple comparisons (P_{adj}). Overall model fit is shown elsewhere (Table 3-3).

(a)	*Microhabitat*	*Day 0*				*Day 30*				*Day 49*				*Day77*			
	Comparison	Est.	SE	T_{152}	P_{adj}	Est.	SE	T_{152}	P_{adj}	Est.	SE	T_{152}	P_{adj}	Est.	SE	T_{152}	P_{adj}
$\log_{10}(AGV)$	C+SS vs. C+IS	0.85	0.14	0.61	0.930	0.06	0.14	0.43	0.973	-0.07	0.14	0.48	0.963	-0.22	0.14	1.53	0.422
	C+SS vs. NC+SS	-0.07	0.16	0.44	0.972	-0.17	0.16	1.07	0.709	**-0.48**	**0.16**	**3.08**	**0.013**	**-0.76**	**0.16**	**4.89**	**<0.001**
	C+SS vs. NC+IS	-0.02	0.14	0.14	0.999	-0.09	0.14	0.61	0.930	-0.25	0.14	1.79	0.283	**-0.38**	**0.14**	**2.71**	**0.037**
	C+IS vs. NC+SS	-0.15	0.14	1.13	0.819	-0.23	0.14	1.67	0.344	**-0.41**	**0.14**	**3.02**	**0.016**	**-0.54**	**0.14**	**3.99**	**<0.001**
	C+IS vs. NC+IS	-0.11	0.12	0.87	0.673	-0.15	0.12	1.22	0.616	-0.19	0.12	1.54	0.414	-0.17	0.12	1.40	0.499
	NC+IS vs. NC+SS	-0.05	0.14	0.35	0.985	-0.08	0.14	0.58	0.938	-0.22	0.14	1.64	0.361	**-0.37**	**0.14**	**2.73**	**0.036**

(b)	*Microhabitat*	*Day 0*				*Day 30*				*Day 49*				*Day77*			
	Comparison	Est.	SE	T_{106}	P_{adj}	Est.	SE	T_{106}	P_{adj}	Est.	SE	T_{106}	P_{adj}	Est.	SE	T_{106}	P_{adj}
RGR	C+SS vs. C+IS	-	-	-	-	-0.03	4.87	0.01	0.999	-6.49	4.87	1.33	0.545	-4.83	4.87	0.99	0.754
	C+SS vs. NC+SS	-	-	-	-	-3.09	4.25	0.59	0.935	**-15.63**	**4.25**	**2.98**	**0.019**	-9.55	4.25	1.82	0.270
	C+SS vs. NC+IS	-	-	-	-	-1.41	4.91	0.29	0.992	-8.43	4.91	1.72	0.320	-3.69	4.91	0.75	0.876
	C+IS vs. NC+SS	-	-	-	-	-3.06	4.65	0.66	0.912	-9.14	4.65	1.97	0.207	-4.72	4.65	1.01	0.741
	C+IS vs. NC+IS	-	-	-	-	-1.38	4.27	0.32	0.988	-1.95	4.27	0.46	0.968	1.14	4.27	0.27	0.993
	NC+IS vs. NC+SS	-	-	-	-	-1.68	4.68	0.36	0.984	-7.19	4.68	1.54	0.420	-5.86	4.68	1.25	0.596

comparisons (Table 3-4b) were only significant for a single comparison on day 49; *RGR* of seedlings transplanted to shrub soils was higher when canopies were absent (NC+SS) than when they were present (C+SS) (Fig. 3-2b; Table 3-4b).

In the survival analysis, larger plants survived better. Cox PH models estimated a 38% lower hazard for each 10-fold increase in the initial *AGV* of the transplanted seedlings being compared (HR = 0.615; $\chi^2_1 = 65.151$; $P < 0.001$). The interaction term was removed from the model since it was not significant ($\chi^2_3 = 4.039$; $P = 0.230$), i.e. the effects of size and treatment were independent. After controlling for plant size by including it as a covariate, results contrasted markedly from those in the seed sowing experiment. Seedlings transplanted in shrub soils had 57% higher hazard than did those in interspace soils when canopies were present (C+SS ÷ C+IS) (Fig. 3-3; Table 3-2b). Similarly, seedlings transplanted into shrub soils had 26% more hazard compared to those in interspace soils if canopies were absent (NC+SS ÷ NC+IS) (Fig. 3-3; Table 3-2b). In contrast to the effects of soil microhabitat, canopy had no significant effect on hazard for plants growing in shrub soils (C+SS÷NC+SS) or in interspace soils (C+IS÷ NC+IS) (Fig. 3-3; Table 3-2b). Of the two natural microhabitats, transplants beneath natural shrubs (C+SS) had 31% greater hazard than transplants in natural interspaces (NC+IS) (Fig. 3-3; Table 3-2b).



* P < 0.05; *** P < 0.001

Fig. 3-3: Pair-wise comparisons of the percentage of transplanted seedlings remaining over time. Significance tests apply to hazard ratios from a Cox PH model (see Table 2b); a significant difference indicates that the risk of mortality in one microhabitat is greater than the other.

Lastly, comparing the two experimentally created microhabitats, transplants in the artificially shaded interspace soils (C+IS) had 34% lower hazard than those in artificially exposed shrub soils (NC+SS) (Fig. 3-3; Table 3-2b). Again, while these early survival differences are interesting, only one transplanted seedling remained in each treatment at the end of the study.

Summary

Soil type had significant but contrasting effects on emerged seedling density and survival, and the effect of soil on survival depended on which experiment was examined (Table 3-5). While the net-effects of canopy were generally weaker than the net-effects of soil, when *P. palmeri* responded to canopy presence, the effects depended on the soil microhabitat, performance metric, and experiment being considered (Table 3-5).

Table 3-5

Summary of the response of emergence, survival, size and growth to canopy presence (relative to absence) and shrub soil (relative to interspace soil) in the two experiments. Effects can be positive (+), negative (−), or neutral (0) and can depend on the microhabitat condition (superscripts). For example, ‘$+^{IS}/0^{SS}$’ indicates that the effect of canopy presence was positive on interspace soils but neutral on shrub soils. Decimals (‘.’) indicate unanalyzed responses

	Seed-sowing experiment		*Seedling-transplant experiment*	
Metric	Canopy presence	Shrub soil	Canopy presence	Shrub soil
Emergence	0	−	.	.
Survival	$+^{IS}/0^{SS}$	+	0	−
Size/Growth	.	.	$0^{IS}/-^{SS}$	$0^{C}/+^{NC}$

V. Discussion

Using a combination of canopy removal and mimicry manipulations, the effects of shrub canopies on *P. palmeri* emergence and seedling performance were isolated from the simultaneous effects of shrub-altered soil. The results suggest that soils beneath shrubs influenced emergence and seedling survival much more than canopy effects, which were only occasionally important and depended on soil conditions. Further, soil-driven seed-seedling conflicts were suggested by the seed sowing experiment.

Seed sowing experiment

Emergence of *P. palmeri* was lower on shrubs soils than interspace soils, suggesting that soils beneath *A. tridentata* had a net negative effect on emergence. That emergence had no apparent response to canopies suggests that canopies had no net effect on emergence. Greater emergence densities in interspace soils were more likely due to higher emergence rates rather than higher seed bank density since initial seed bank density was controlled for and most studies find that seeds accumulate under shrubs rather than their interspaces (Pugnaire and Lázaro 2000). Other research on natural *P. palmeri* emergence patterns and germination requirements indicate *P. palmeri* seeds require sufficient light, temperatures, and moisture to break dormancy and can form persistent seed banks when seeds are buried (Kitchen and Meyer 1992; Meyer and Kitchen 1992). However, heat can overcome light requirements allowing buried seeds to germinate (Kitchen and Meyer 1992). Therefore, if seeds become trapped and buried by shrub soils and litter, they may not germinate during dry years. Instead they may persist in the seed bank until soils are disturbed or if sufficiently warm temperatures break seed dormancy preceding a 'biologically significant' (Reynolds et al. 2004) precipitation event, triggering a pulse of germination (Noy-Meir 1973). Even if seeds do germinate, litter can also act as a physical barrier to emergence, or as a chemical inhibitor due to allelopathic leachates (reviewed in Facelli & Picket 1991). Greater seed predation in shrub soils could possibly also reduce shrub soil seed bank density if belowground seed predators prefer foraging in litter (e.g. herbivorous anthropods in Facelli 1994), but for above ground seed predators, higher seed predation under shrubs is usually attributed canopies providing seed consumers from their predators (Castro et al. 1999; Hulme and Borelli 1999; Vander Wall and Thayer 2001; Callaway 2007 pp 117-178; Barbosa et al. 2009). However, canopies had no effect on emergence density suggesting that such indirect biotic interactions are absent or they are masked by simultaneous positive canopy effects. Given the light and temperature sensitivity of dormant *P. palmeri* seeds (Kitchen and Meyer 1992), it is surprising that canopies had no detectable influence on emergence. However, *A. tridentata* canopies are known to have lasting indirect effects on soils (Bechtold and Inouye 2007) and in this study *A. tridentata* soils appeared to suppress *P. palmeri* emergence, though the mechanisms remain unclear.

Emerged seedling survival was higher in shrub soils, regardless of canopy presence or absence, suggesting that the positive effects of shrubs soils on seedling survival might outweigh their negative effects. For example, while *A tridentata* litter can have allelopathic effects (Schlatterer and Tisdale 1969; Weaver and Klarich 1977; Kelsey et al. 1978), long-term improvements of nutrient availability (Bechtold and Inouye 2007) and subsequent increased beneficial microbial activity (van der Heijden and Horton 2009; Bashan and de-Bashan 2010), may be more important for *P. palmeri* seedling survival; however, the fact that post-emergence survival was higher on shrub soils suggests allelopathic effects were probably not important unless they negatively influence emergence but had no effect on seedlings. Canopy presence had no effect on survival when seedlings emerged in shrub soils, but those that emerged in interspace soils benefitted from canopy presence suggesting that canopies, even the leafless experimental canopies present when seedlings emerged, have net positive effects on seedling survival in interspace soils but the positive and negative effects of canopies were balanced in the presence of shrub soil. If lower survival in interspace soils indicated stressful conditions, then observing a net-positive effect of canopy on survival in stressful interspace soils but a neutral effect of canopy in shrub soils suggests that the positive effects of shrubs are more pronounced under stressful conditions; this pattern is consistent with the SGH (sensu Bertness & Callaway, 1994). However, most experimental studies have not detected this type of interaction since they examined differences between shrub and interspace soils only in the presence of shelter, as in canopy mimic experiments (Holzapfel and Mahall 1999; Padilla and Pugnaire 2008; Becerra and Bustamante 2011) or absence of shelter, as in canopy removal experiments (Callaway 1992; Callaway et al. 1996). One study also combined shrub removal and canopy mimicry to evaluate the independent and interacting effects of shade and soil (Gómez-Aparicio et al. 2005). While they did not examine emergence patterns, their results suggested that both canopy presence and shrub soil microhabitat improved transplanted tree seedling performance, but the effects of shade were much more important than soil (Gómez-Aparicio et al. 2005). A relevant greenhouse study (Carrillo-Garcia et al. 2000) took soil from beneath mesquite (*Prosopis articulata*) and from interspaces and used it as a potting medium for the columnar cactus, cardon (*Pachycereus pringlei*). Cardon potted in these different soil microhabitats were then grown beneath either 50% shade simulation (canopy mimic via shade cloth), or in full sun; their results were strikingly similar to the results found here (Carrillo-Garcia et al. 2000). They also found that 'resource island' tree soil had strong positive effects on survival, regardless of whether shade cloth was present, and that shade cloth greatly influenced survival, but only when cactus grew in interspace soils; they concluded that survival depends on the interacting effects of shade and soil (Carrillo-Garcia et al. 2000). The result from this study, and others (Carrillo-Garcia et al. 2000; Kitzberger et al. 2000; Gómez-Aparicio et al. 2005) suggest that the effects of canopy and soil are often not independent of each other, and should be more often be studied in a fully factorial manner.

Seedling emergence and survival responded to soil microhabitat in a conflicting manner, with shrub soils reducing emergence density but also increasing emerged seedling survival relative to interspace soils. These results suggest a soil driven seed-seedling conflict in which the soil conditions that were unfavorable for the seed stage were later favorable for the seedling stage. Seed-seedling conflicts are common throughout many ecosystems (Schupp 1995). Similar patterns were found in a study demonstrating that *C. ledifolius* litter reduced the emergence of experimentally sown *C. ledifolius* seeds, probably since litter created a physical barrier, but litter improved survival of transplanted seedlings, possibly since litter improved the soil microclimatic conditions (Ibáñez and Schupp 2002). Further, results of a canopy mimicry experiment (shade cloth) suggested that shade increased emergence of sown seeds, perhaps through increased soil moisture , but that survival was higher in interspace soils with canopies (mimics) than in shrub soils with canopies (Becerra and Bustamante 2011). This result may have been due to allelopathic effects of litter; while their design could not address the effects of soil in the absence of shade, their results suggest that the order of seed-seedling conflicts can be opposite from what was observed in this study (i.e. positive effects of shrubs on emergence, but negative on survival) and that positive effects may occur through different mechanisms than negative effects (Becerra and Bustamante 2011).

Seedling transplant experiment

Transplanted seedlings in each microhabitat were initially similar in size, but by day 49 plant size differed between some microhabitats and these differences were even greater by day 77. Only seedlings transplanted to shrub soil with no canopy treatment (NC+SS) grew in size between day 49 and day 77 suggesting a net-negative effect of canopy; however, in interspace soils, canopy presence had no effect on transplanted seedling size. Further, shrub soil only had positive effects on growth in the absence of canopies, suggesting that soils are favorable for growth, but only in the absence of negative canopy effects. These results demonstrate that the response of growth under canopies can depend on soil microhabitat and the effect of soil microhabitat can depend on canopy presence or absence; other factorial examinations of shade and soil have observed similar interactions between canopy and soil effects (Carrillo-Garcia et al. 2000; Gómez-Aparicio et al. 2005). Despite nearly double the precipitation in 2009 and water supplementation, growth (*RGR*) was generally negative, suggesting that seedling transplants struggled to maintain biomass. However, there was one exception: seedlings transplanted to shrub soils without canopies (NC+SS) grew between June-July 2009 (day 49-77) and by day 49, they grew faster in this microhabitat than in shrub soils with canopies, where transplanted seedling shrunk throughout the study. Otherwise, growth was rarely different between microhabitats and censuses despite significant model effects for microhabitat and time (days since transplant) in the *RGR* model and large size differences developed by day 77 in the *AGV* model; this suggests that undetected differences in *RGR* resulted in significant cumulative differences in *AGV*, highlighting the importance of examining both.

Compared to analyses of emergence and survival, analyses of size and growth have been less examined in removal or shrub mimicry experiments (but see Callaway 1992; Callaway et al. 1996; Kitzberger et al. 2000; Gómez-Aparicio et al. 2005). One removal experiment revealed a negative effect of shrub canopies on transplanted tree seedling growth in *A. tridentata* soils (Callaway et al. 1996). Separate shrub mimicry experiments showed that artificial shade reduced seedling growth (Callaway 1992), but these experiments in isolation examined interactions only within particular soil microhabitats, not between them. Therefore, these experiments could not assess the potentially interacting effects of shade and soil on growth, like those observed in this study and others (Carrillo-Garcia et al. 2000; Gómez-Aparicio et al. 2005). Another experiment combining shrub mimicry and shrub removal demonstrated that growth effects of shrubs were rare for understory tree species, but that one tree (*Quercus ilex*) species had complex growth responses to shade and soil (Gómez-Aparicio et al. 2005). More specifically, shade appeared to have an overall positive effect on growth, independent of soil type, but shrub soil only had positive effects on growth in the presence of a canopy; the response of growth to soil microhabitat depended on canopy presence or absence (Gómez-Aparicio et al. 2005). The effects of shade on seedling growth in their experiment were positive, regardless of soil microhabitat. However in the present experiment, the effects of shade on growth were negative, and required the presence of shrub soils to be apparent. Further the effects of soil on seedling growth in their study were only apparent in the presence of shade while the effects of shrub soil on growth in the present study were only apparent in the absence of shade. While the specific effects of canopies and soils were very different between these studies, they shared an important interaction between shade and soil that could only be revealed when shrub removal and canopy mimicry experiments were combined. It should be noted here that there are other ways to address the interacting effects of canopies and soils.

Survival of transplanted seedlings was not influenced by shrub canopies in either soil microhabitat; however, survival in shrub soils was always lower than survival in interspace soils regardless of canopy presence or absence on either soils microhabitat. This suggests that the negative effects of shrub soils on transplanted seedling survival outweighed their positive effects. This result, combined with the positive effects of shrub soils on growth, suggests a conflict between survival and growth due to soil microhabitat; transplanted seedlings in shrub soils had lower survival than those in interspace soils, suggesting that soil conditions were unfavorable for establishment, but once established, growth was higher in shrub soils than in interspace soils. In a removal experiment, a similar conflict between survival and growth occurred by canopy-related mechanisms; survival of *Pinus monophylla* was higher under *A. tridentata* canopies than in the open or removed microhabitats, probably due to shrubs favorably altering microclimate and providing associational defense, but the positive effects of shelter simultaneously negatively influenced growth (Callaway 1992).

Contradictions between experiments

While the seed sowing and transplant experiments both indicated that soil microhabitat generally influenced seedling survival more than canopy presence, the response of seedling survival to soil microhabitat was opposite in the two experiments; the effect of soils on survival was positive in the sowing experiment but negative in the transplant experiment. Negative soil effects in the transplant experiment but not the sowing experiment suggest that experimental differences altered the outcome of seedling survival. Monsoonal conditions were wetter than average during early days of the transplanted seedling survival observations (2009) but during observations of emerged seedling survival in the seed sowing experiment (2010), monsoonal precipitation was below average. Negative effects of shrub soils on transplanted seedling survival also may have arisen due to the addition of water; for example, litter could retain the added water, preventing it from infiltrating to plant roots (Facelli and Picket 1991). These experimental differences in water availability, could influence the outcome of plant interactions (e.g. Greenlee and Callaway 1996; Kitzberger et al. 2000; Tielbörger and Kadmon 2000), which are predicted by the SGH to become increasingly negative as conditions become less stressful with water addition (Bertness and Callaway 1994). While transplant experiments permit control over some factors (plant size, density, and spatial arrangement), they can be challenging to establish and interpret, requiring manipulatively balancing water requirements of plants to prevent transplant shock (see Close et al. 2005) without altering the outcome of the interactions under investigation (Kitzberger et al. 2000; Padilla and Pugnaire 2008). In contrast, relative to transplant experiments, seed sowing experiments can be more informative about seed-seedling conflicts and require less effort, but in arid environments, if water is not supplemented, it may take years for a precipitation event to be large enough to trigger a pulse of germination (Noy-Meir 1973; Reynolds et al. 2004). Nonetheless, seed-sowing results closely matched natural patterns of lower emergence but higher survival under shrubs compared to interspaces (Chapter 2). Thus, the survival results of the seed-sowing experiments are probably more reliable than the survival results of the seedling-transplant experiment.

Demographic implications

Understanding the demographic consequences of these results requires a better understanding of the relationship between seed bank dynamics, seed-seedling conflicts, and facilitation. Ultimately, all seedlings died by the end of the seed sowing experiment and only one seedling remained in each treatment of the seedling transplant experiment suggesting that *P. palmeri* establishment was severely limited in 2010. This may have been due to 2010 winter precipitation being above average (2000-2008), possibly triggering a pulse of germination with spring snowmelt, followed by summer precipitation being half the mean, probably causing rapid seedling mortality. If the negative effect that shrub soils had on emergence densities is due to reduced emergence rates (rather than reduced seed bank density) and seeds that did not germinate during the study remain viable, then the observed negative effect of shrubs on single-season emergence rates suggest a positive long-term effect of shrubs on *P. palmeri* seed bank persistence.

Interspace soils were associated with improved seedling emergence but reduced seedling survival while shrub soils were associated with reduced seedling emergence but improved seedling survival. This suggests that the order of seed-seedling conflicts was reversed for shrub and interspaces soil microhabitats. While both soil microhabitats had poor establishment rates due to either reduced emergence or reduced survival, the order of the seed-seedling conflict has important implications for seed bank persistence in different soil microhabitats. In interspace soil, a conflict of high emergence densities followed by low survival is expected to deplete the seed bank, but in shrub soils, a conflict of low emergence densities followed by high seedling survival should have positive consequences for long-term seed bank persistence if seed survive and remain viable. These results add to a growing body of evidence showing the positive effects that shrubs may have on seed bank persistence in arid and semi-arid ecosystems (Pugnaire and Lázaro

2000); however, the implications of seed-seedling conflicts for seed bank persistence and, therefore population stability, remain poorly understood.

Conclusion

Experimental manipulations of shade narrowed the range of mechanisms that may be driving natural patterns of *P. palmeri* emergence and performance. Soil properties had important but conflicting roles in emergence, survival, and cumulative growth (i.e. size) of *P. palmeri*; in contrast, shrub canopies often had relatively weak effects on *P. palmeri* emergence and performance and the effects of canopies depended on soil conditions. However, it remains unclear which properties of shrub soils are responsible for the observed patterns. Integrating concepts of facilitation, seed-seedling conflicts, and seed bank persistence could help describe the spatio-temporal heterogeneity of plant populations and the demographic consequences of interspecific associations in arid and semi-arid ecosystems. Future research should investigate how the order of seed-seedling conflicts vary along gradients of environmental stress (Schupp 2007) and the effect of the order of the seed-seedling conflict on persistence of seed banks.

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CHAPTER 4

USING STRUCTURAL EQUATION MODELING TO EXPLORE REPRODUCTIVE CONSEQUENCES OF ASSOCIATIONS BETWEEN A PERRENIAL FORB (*PENSTEMON PALMERI* A. GRAY) AND A SHRUB (*ERIODICTYON ANGUSTIFOLIUM* NUTT.) IN THE MOJAVE DESERT

I. Abstract

For decades ecologists have investigated the various interactive factors of plant reproductive ecology, but few have examined the direct and indirect effects of facilitation on plant reproductive ecology. Reproductive output can be limited by a suite of potentially highly correlated factors (e.g. water stress, pollen limitation, resource allocation). In deserts, overstory plants can improve the water use efficiency of plants growing beneath their canopies, yet few studies investigate how facilitation of water use efficiency might influence understory reproduction. Similarly, the reproductive importance of pollinator behavior is well documented, yet studies considering how overstory plants might influence pollinator foraging behavior on understory plants are lacking. Here, I used structural equation modeling to explore how spatial association with overstory shrubs of *Eriodictyon angustifolium* might influence the single-season seed production of an understory short-lived perennial herb (*Penstemon palmeri)*. Two broad questions are addressed: 1) how does association with *E. angustifolium* influence single-season *P. palmeri* seed production? 2) Which direct and indirect factors are responsible for any differences? Results indicate shrubs had a net-negative effect on *P. palmeri* seed production due to shrubs strongly reducing the size of *P. palmeri*, indirectly limiting total bud initiation and nectar production, which were factors that were related to pollinator visitation and thence fruit production. However, the strong negative effects of shrubs on understory seed production coincided with decreased understory water stress, fewer aborted buds, and a greater percentage of

bees choosing to forage for pollen. These results suggest that overstory shrubs suppressed the growth of *P. palmeri*, but they simultaneously facilitated *P. palmeri* by reducing water stress and increased foraging activity for pollen by bees, leading to a weak mitigation of the negative effects of shrubs on plant size. Further, larger plants had more mature fruits, but the frequency of visits during which bees collected pollen corresponded with an increase in the number of mature fruits, suggesting that *P. palmeri* is resource limited, but also pollen limited.

II. Introduction

A renewed interest in positive interactions, especially facilitation, in the past 15 years has led to greater understanding of ecological systems (Brooker and Callaway 2009). Many ecological concepts were developed before it was recognized that facilitation can be a key force shaping communities (Bruno et al. 2003). Mutual progress has been made by merging the conceptual framework of facilitation with better understood frameworks, such as niche theory (Bruno et al. 2003), phylogeny (Valiente-Banuet and Verdú 2008), life-history strategy (Maestre et al. 2009), and functional traits (Butterfield and Briggs 2011). The field of plant reproductive ecology provides a conceptual framework to describe patterns and strategies of reproduction, and has been studied intensively (see Stephenson 1981; Doust and Doust 1988); the reproductive importance of plant size (Bonser and Aarssen 2009; Weiner et al. 2009), pollinator behavior (Zimmermann 1988), competition (Weiner 1988) and herbivory (Hendrix 1988) are fairly well documented. However, relatively few studies of reproduction have included facilitation as a potentially influential factor of reproduction (Brooker et al. 2008) and those that have (Casper 1996; Shumway 2000; Tielbörger and Kadmon 2000; Choler et al. 2001; Kikvidze et al. 2001; Tirado and Pugnaire 2003; Griffith 2010; Soliveres et al. 2010; Cranston et al. 2012) did not address the potential influence of facilitation on pollinator behavior, floral display and reward, or the fate of buds as they mature into fruits. As a consequence, the evolutionary impact of facilitation is often overlooked as a consequence of poor understanding of the fitness response of plants to facilitation (Brooker et al. 2008; Bronstein 2009)

Positive and negative interactions between plants are thought to occur simultaneously (Bertness and Callaway 1994; Callaway 1995, 2007 pp 179-254; Callaway and Walker 1997; Maestre et al. 2003) and both can act directly or indirectly and a through multitude of interacting physical, biotic, and chemical mechanisms (Callaway 2007 pp 15-178). Net interactions between plants are predicted to be increasingly facilitative as environments become more biotically and abiotically severe (Bertness and Callaway 1994). Though this ‘stress gradient hypothesis’ (sensu Bertness and Callaway 1994) is well supported, there are exceptions (reviewed in Brooker et al. 2008); these differences largely arise due to variable effects of stress gradients on different life-stages (Miriti 2006; Schiffers and Tielborger 2006; Armas and Pugnaire 2009; Soliveres et al. 2010) and traits of interacting plant pairs (Callaway 2007 pp 255-292; Butterfield and Briggs 2011). Extending these patterns to reproduction suggests that, the importance of facilitation on reproduction should depend on the environmental conditions plants face during reproduction (e.g. Casper 1996), the sensitivity of various stages of reproduction (budding, flowering, and fruiting) to those conditions, and the degree to which different stress factors can be mediated by benefactor (facilitating plant) and beneficiary (facilitated plant) traits (sensu Callaway 1995).

Plant size is closely related to the energy and resources that are available to reproduction (Stephenson 1981; Reekie and Bazzaz 1987; Weiner et al. 2009) and reproductive effort in plants is costly (Obeso 2002), requiring an investment of resources to developing buds, flowers (and their nectar and pollen), and fruits (Stephenson 1981). To manage these costs, plants abort reproductive parts, allowing resources to be translocated to more developed parts if resources become limited (Stephenson 1981). By definition, water is limited in deserts, so if shrubs ameliorate water stress, as they can in arid environments (Maestre et al. 2003; Gómez-Aparicio et al. 2004), plants growing under shrubs may demonstrate different patterns and strategies of abortion than their potentially water-limited neighbors in interspaces. A water-limited plant is expected to benefit most by aborting the least developed flowers (i.e. buds) since less water has been devoted to their development (i.e. the loss of the structure is less costly) and a portion of invested water (and other resources) can be translocated to further developed floral structures that are more developed (i.e. flowers, fruits, and/or seeds) (Stephenson 1981). If shrubs reduce water limitation, rates of abortion may be lower, leading to an indirect increase in successful fruit maturation, but research examining patterns of abortion in the context of facilitation is lacking.

Although resources often limit individual seed production and fruit set (Stephenson 1981), pollination can also be limiting (Rathcke 1983; Zimmermann 1988; Larson and Barrett 2000; Knight et al. 2005).The importance of pollen limitation depends on specific plant traits (e.g. floral display size, longevity, ovules per flower) and life-history strategy (i.e. iteroparity vs. semelparity) among other factors (Larson and Barrett 2000; Knight et al. 2005). By investing resources to floral display and nectar rewards, plants can decrease pollen limitation by influencing decisions made by pollinators, such as whether to visit, how long to stay, and where to go after visiting (Zimmermann 1988). There is substantial evidence that pollinators forage optimally (see Pyke 1984 for review); in order to maximize fitness they behave in ways that increase the forage collected while reducing the costs of collecting it (MacArthur and Pianka 1966; Charnov 1976). Thus, plants with larger floral displays tend to attract more pollinators since pollinators can rapidly acquire floral resources while minimizing the travel costs between flowers (Galen 1999). Nectar production has been thought to have limited influence on visitation rates since assessing the reward requires a pollinator to visit a plant (Zimmermann 1988); however, olfaction in *Osmia* spp. bees permits detection of nectar prior to visiting flowers (Howell and Alarcón 2007), suggesting that plants that produce copious nectar may be able to attract certain pollinators from a distance. How pollinators respond to an individual's floral display and rewards depends on whether conspecific and heterospecific neighbors compete for or facilitate visitation. Examples of both competition for, and facilitation of pollination, are well documented (Rathcke 1983; Ghazoul 2006); however, it is unknown how overstory desert plants may directly or indirectly influence pollinator behavior. Higher densities of flowering plants are expected if their survival is facilitated, thus facilitation of survival may indirectly influence the intensity of interactions for pollination. In arid Mediterranean ecosystems, nectar volume and concentration is driven by plant traits and abiotic conditions, i.e. temperature, humidity, light intensity, water availability and nutrient stress (Petanidou 2007). If shrubs alter these conditions to be more favorable, then plants growing beneath their canopies may produce more nectar. Such an effect could also increase patch-scale reward, potentially altering foraging decisions of pollinators. Floral microclimate, such as temperature and relative humidity, has been shown to be an important determinant of bee foraging behavior (Herrera 1995a, b; Rands and Whitney 2008). Thus, since shrubs can buffer climatic extremes via canopy structure (Tracol et al. 2011), they may consequently alter foraging behavior of bees, especially in environments where climatic conditions are extreme and highly variable throughout the day.

In reality, fruit set is often not limited by a single factor, but instead by a combination of highly interrelated and temporally variable factors (Lee 1988; Campbell and Halama 1993; Mitchell 1994). The number of ovules produced, the amount and quality of pollen delivered to stigmas, the amount of resources available for fruit and seed filling, herbivory, predation, disease, and the physical environment can all limit reproduction simultaneously or asynchronously (Stephenson 1981) and are not mutually exclusive (Lee 1988). Such complexity might benefit from a multivariate approach for inference. Structural equation modeling (SEM) is an extension of path analysis that allows for explicit modeling of error terms, multicollinearity, and goodness of fit. It is well suited for situations where the interest lies in determining relative importance of direct, indirect, and total effects of different factors on the response of interest (see Grace 2006).

For these reasons, SEM has been used to evaluate multiple simultaneous determinants of seed production (Campbell and Halama 1993; Mitchell 1994).

The objective of this study was to use SEM to explore the direct and indirect consequences of interspecific interactions between the herbaceous perennial *Penstemon palmeri* (A. Gray) and the shrub *Eriodictyon angustifolium* (Nutt.) on the reproduction of *P. palmeri*. I asked two questions: 1) Does association with *E. angustifolium* positively or negatively influence single-season *P. palmeri* seed production? 2) Which direct and indirect processes might be responsible for those differences? Natural observations at this site suggested that in the presence of *E. angustifolium,* adult *P. palmeri* survived better and bud-to-fruit maturation success was greater, but fewer *P. palmeri* initiated flowering (Chapter 2). Consequently, relative to interspaces, plants located under shrubs are likely to have closer neighbors (due to increased survival), but have lower water stress. Plant size is expected to be the most important determinant of seed production, but water limitation, and pollinator foraging behavior are expected to be important as well. The effects of water stress in *P. palmeri* are unknown, but water stress is expected to negatively impact nectar production, reproductive maturation, and ultimately seed production. The least developed floral structures (i.e. buds) are expected to be most impacted by water limitation. It is unclear how the presence of *E. angustifolium* might directly influence pollination, but the potential for shrubs to alter visitation rates or foraging behavior upon individual plants are investigated. Three major groups of factors important in seed production were considered: plant-plant interactions (e.g. the effects of shrub presence and conspecific density on water stress and plant size), plant-pollinator interactions (e.g. the effects of local flower density on visitation rates and foraging behavior), and reproduction ecology (e.g. the number of initiated buds, and the fate of those buds). The effects of these groups of factors on each other were also examined (e.g. the effects of visitation rates on fruit and seed production).

III. Materials and Methods

Study site

Observations were made from May-November 2009 in Lovell Canyon within the Mojave Desert shrublands in the southern range of the Spring Mountains ~30 km west of Las Vegas, NV (latitude: 36° 9' 11.663" N; longitude: 115° 34' 19.515" W; elevation = 1770 m). The site burned 7 years prior, and line-point cover estimates (Chapter 2) indicate that the vegetation consisted of a diverse mixture of nine Mojave Desert shrub species covering 50-60% of the area; *E. angustifolium* was the dominant shrub, responsible for roughly 70% of total shrub cover (Chapter 2). Other herbaceous perennials and some grasses occurred throughout. Soil associations from the USDA NRCS web soil survey (Soil Survey Staff et al. 2011) indicate soils are Purob-Irongold associated; soils are well drained shallow gravelly loam with a deep water table (~2 m) with a shallow petrocalcic layer (~50 cm).

Climatic data

Estimated mean annual temperature and mean annual precipitation were obtained for 2000 - 2009 (PRISM Climate Group 2011). In 2009 the site received 297 mm of precipitation, ~13% lower than the mean annual precipitation from 2000-2008 (340 mm), and annual temperature for 2009 was 11.6 °C, very similar to the mean annual temperature from 2000-2008 (11.9°C). Winter precipitation (November 2008-April 2009) was considerably greater than the average from 2000-2008 (289 mm; mean = 198 mm). May was a relatively wet month (17 mm; mean = 3 mm), and June was very dry as usual (< 1 mm; mean < 1 mm). July had stronger than usual monsoonal precipitation (38 mm; mean 29 mm), but August-October had below average precipitation making for a shorter than normal monsoon season (August: 7 mm, mean = 35 mm; Sept: 7 mm, mean = 18 mm; Oct: 2 mm, mean = 32 mm).

Species of interest

Suspected Beneficiary: Palmer's penstemon (*P. palmeri*) is a native perennial forb that produces brilliant displays of white and purple flowers. Inflorescences develop acropetally and can support hundreds of flowers with buds initiated throughout the reproductive season. In 2009, flowering within the population began before data collection, most likely beginning in late April to early May. Flowering continued through June, but many flowers began to rapidly wither and detach toward the month's end. By mid-July, flowering ceased. Fruits (i.e. capsules) matured between September and October. By November all capsules had dehisced.

Suspected Benefactor: Yerba Santa (*E. angustifolium*) is a native perennial shrub that produces flowers from June to July and occurs throughout the arid United States Southwest in washes and on slopes (Baldwin et al. 2002). These shrubs can grow to over 2 m and the major diameter of their canopy can span several meters. Yerba Santa shares many floral visitors with *P. palmeri* (personal observation). All plant names follow the USDA NRCS PLANTS database (NRCS 2011).

Pollinators: Observations indicate that bees are the primary visitors to *P. palmeri* from dawn to dusk; a single hummingbird was observed feeding on nectar of a *P. palmeri* not involved in the study. Bees were identified by Dr. Terry Griswold and vouchered in the United States Department of Agriculture Pollinating Insect Collection at Utah State University. In the field, between 830-1730 hr, 1-2 genera of small bees [*Ceratina* sp. or *Ashmeadiella* sp.] actively foraged for pollen and nectar independently; these were impossible to distinguish in the field since they were similar in size and color. Their small size permitted entry into the corolla without contacting the anthers on the dorsal interior surface of the corolla. This allowed them to potentially access nectaries (between the base of the anther filaments and the interior corolla) without pollen transfer; however, these species sometimes chose to forage for pollen and when they did, pollen transfer would have been possible. In contrast, when foraging for nectar, larger bees (*Xylocopa tabanaformis, Anthophora* sp.) and vespoid wasps (Vespidae) had to enter the corolla by passing the staminode, promoting contact between the bee's scopa and the anthers of *P. palmeri*; these larger visitors were extremely rare (0.92% of all observed visitors) during observations compared to the smaller visitors that actively foraged for pollen.

Data Collection

In June 2009, 54 reproductive *P. palmeri* were randomly selected for observation and measurement. Half were located under canopies of *E. angustifolium* and half in interspaces between shrubs. Independence was promoted by selecting *P. palmeri* at least 5m apart. Caudex diameter (the woody stem connecting the roots to the rosette) was measured with calipers and used as an index of plant size; support for this approach comes from another study in which aboveground dry mass of seedlings grown in greenhouses was highly correlated with their caudex diameter (Poulos and Rayburn in preparation; Appendix A). Distances to each of the nearest three conspecific neighbors were measured and averaged ('Average neighbor distance') and used to indicate the potential intensity of intraspecific interactions.

To account for variability of pollinator activity throughout the day, each *P. palmeri* was randomly assigned to one of three groups. Each group consisted of 9 plants under shrubs and 9 in interspaces (18 plants per group). Groups were randomly assigned to one of three time blocks of 6 consecutive days in June: the first block was 11-16 June, the second was 18-24 June, and the third was 25-30 June. Each day within a block was then divided into three observation periods: morning (830-1130hr), early afternoon (1130-1430hr), and late afternoon (1430-1730hr). Observations and measurements for the 18 plants within each group were rotated so that each plant was observed for 2 consecutive days per observation period (6 days total).

On each day, I counted the number of open flowers on each *P. palmeri* plant and the number of open conspecific flowers of other individuals within 1.5 m of each plant ('local flower density'). Pollinator activity was then observed for 12 minutes per day per plantfor 6 days (72 minutes total), with 30 minutes between the start of each observation. During each 12 minute period, the numbers of bees foraging for nectar and/or pollen ('No. foraging bees') were counted. Small bees that actively foraged for pollen were distinguished from those visiting only for nectar to calculate the percentage of bees that foraged for pollen. When the rare larger bee species visited, they were counted as foraging for both nectar and pollen. To minimize disturbance of pollinator activity, observations were made from a distance of 1.5 m, dull colors were worn, and care was taken to remain motionless. Occasionally, some flowers were not observable from a single position because flowers face multiple directions, so it was sometimes infeasible to track visitation patterns on plants with many open flowers. To account for these constraints, the ratio of the total open flowers to observed flowers was multiplied by the total number of bees foraging and the total number of forages for pollen to rescale observations to the whole plant; this assumes that foraging behavior of bees on observed flowers was equivalent to their behavior on unseen flowers.

On the 1st, 3rd, and 5th days of observation, after observing pollinator visitation, a single flower on each plant was randomly selected for nectar measurements. Nectar was first drained using micropipettes. Then the flower was enclosed in spun-bound polypropylene (85% light permeability) to exclude floral visitation. A day later, before observing pollinator visitation, the covering was removed and accumulated nectar was again drained and the volume (μl) recorded.

On 18 July 2009, the second leaf set below the lowest flower of the tallest raceme was collected from each plant to be analyzed for carbon isotopic content, which can indicate water stress (Farquhar et al. 1989). Standardizing collection in this way improves the likelihood that the leaves are of similar age and have experienced similar macroclimatic conditions. The tissue was oven dried at 60ºC for 48 hours and ground to a very fine powder using a mortar and pestle. Each sample(3.5-3.7mg) of the tissue was processed using continuous-flow direct combustion and mass spectrometry on a Europa Scientific SL-2020 system. These $\delta^{13}C$ measurements represent the ratio of $^{13}C/^{12}C$ relative to the standard Pee Dee Belemnite value and were then converted to carbon isotope discrimination (CID) values using this equation (in Farquhar et al. 1989): $\mathrm{CID} = \frac{-8 - \delta^{13}\mathrm{C}}{1+\delta^{13}\mathrm{C}/1000}$. Smaller CID values indicate limited stomatal conductance, a response to water limitation (Farquhar et al. 1989), suggesting greater water stress.

Counts and fates of initiated *P. palmeri* buds during the 2009 season were tracked for each plant. On 3 August 2009, well after pollination had ceased and fruit maturation had begun, the number of pedicles was counted and the fate of the attached reproductive organ was determined where possible. Fates were classified as aborted buds, flowers or fruits, consumed fruits, or mature fruits. Aborted buds were defined as the dry remnants of an unopened, undeveloped, bud. Aborted flowers were defined as the dry remnants of previously open corollas or calyces containing uninflated ovaries; note that under this definition, counts of aborted flowers potentially include both fertilized and unfertilized flowers. Pedicles that had no attached organ were assumed missing due to consumption. Since there was no evidence of herbivory prior to the fruiting stage, these were assumed to be consumed developing fruits, not flowers or buds. The developing fruits of each plant were covered with the same material used to prevent floral visitation in order to catch falling seeds before dispersal. Capsules were collected on 5 November 2009, well after seed maturation was complete. The contents of each capsule were then emptied and the number of mature seeds counted. Seed maturity was tested non-destructively by applying a very small amount of force to a suspected seed using a thin chemical spatula. Seed coats without embryos crush with little effort whereas seed coats with developed embryos require excessive force to crush; this method was validated by dissecting several uncrushed seeds to verify the presence of filled endosperm. A small proportion of capsules had clear evidence of herbivory, but the number of seeds lost to damage was undeterminable; these were counted as mature fruits if they had at least one mature seed. Total bud initiation was assumed equal to the number of pedicles, i.e. the sum of all bud fates.

Data Analysis

An exploratory 'thinning' approach to structural equation modeling (SEM) was taken to seek a more parsimonious model that described the data equally well as, or better than, an a priori model. In SEM, the null hypothesis for the overall model fit (χ^2) is that there is no significant difference between the model predictions and the data. 'Thinning' a pathway forces its estimate (β) to zero, eliminating the need for estimation and increasing the degrees of freedom (df) by 1. Since the fit statistic follows a χ^2 distribution, determining if a pathway significantly improves model fit is achieved by examining the difference in χ^2 between the thinned and unthinned model and using degrees of freedom equal to one ($\Delta\chi^2_{\mathrm{df=1}}$); if $\Delta\chi^2_1$ exceeds 3.84, the critical value corresponding to an $\alpha = 0.05$, then it significantly contributes to overall model fit. Thus, thinning maintains or reduces the χ^2 statistic while increasing degrees of freedom. It has been suggested that even insignificant pathways that contribute little to overall model fit can be justifiably retained if they have strong empirical support in previous studies (Grace 2006). Thus, thinning of models was accomplished by removing pathways contributing little to model fit, starting with the largest *P*-values, and reevaluating after elimination until only significant ($P < 0.05$) paths, or insignificant paths with strong theoretical support, remain.

Three sub models were explored (Fig. 4-1), thinned, and then integrated into a full 'linked' model (Fig. 4-2) which was then explored and thinned. The first sub model explores plant-plant interactions and their consequences for plant size and water stress. A second sub

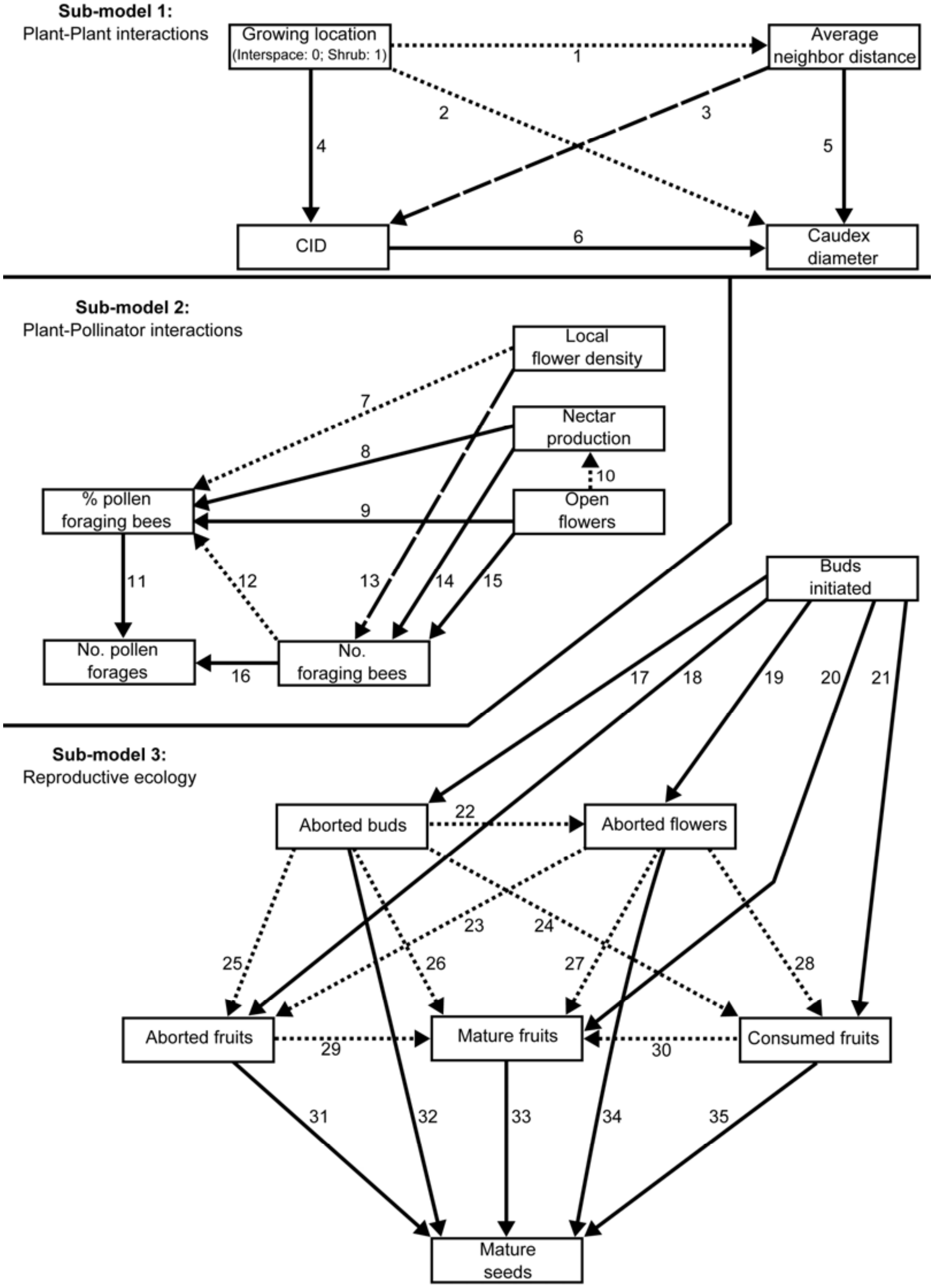

Fig. 4-1: Hypothesized causal relationships within sub-models. Arrows represent the effect of one measured variable on another. Dotted or solid arrows indicate expected negative or positive relationships, respectively. Theoretical and empirical support for each pathway is summarized in the methods section (also see Appendix B). For hypothesized effects between sub-models see Fig. 4-2.

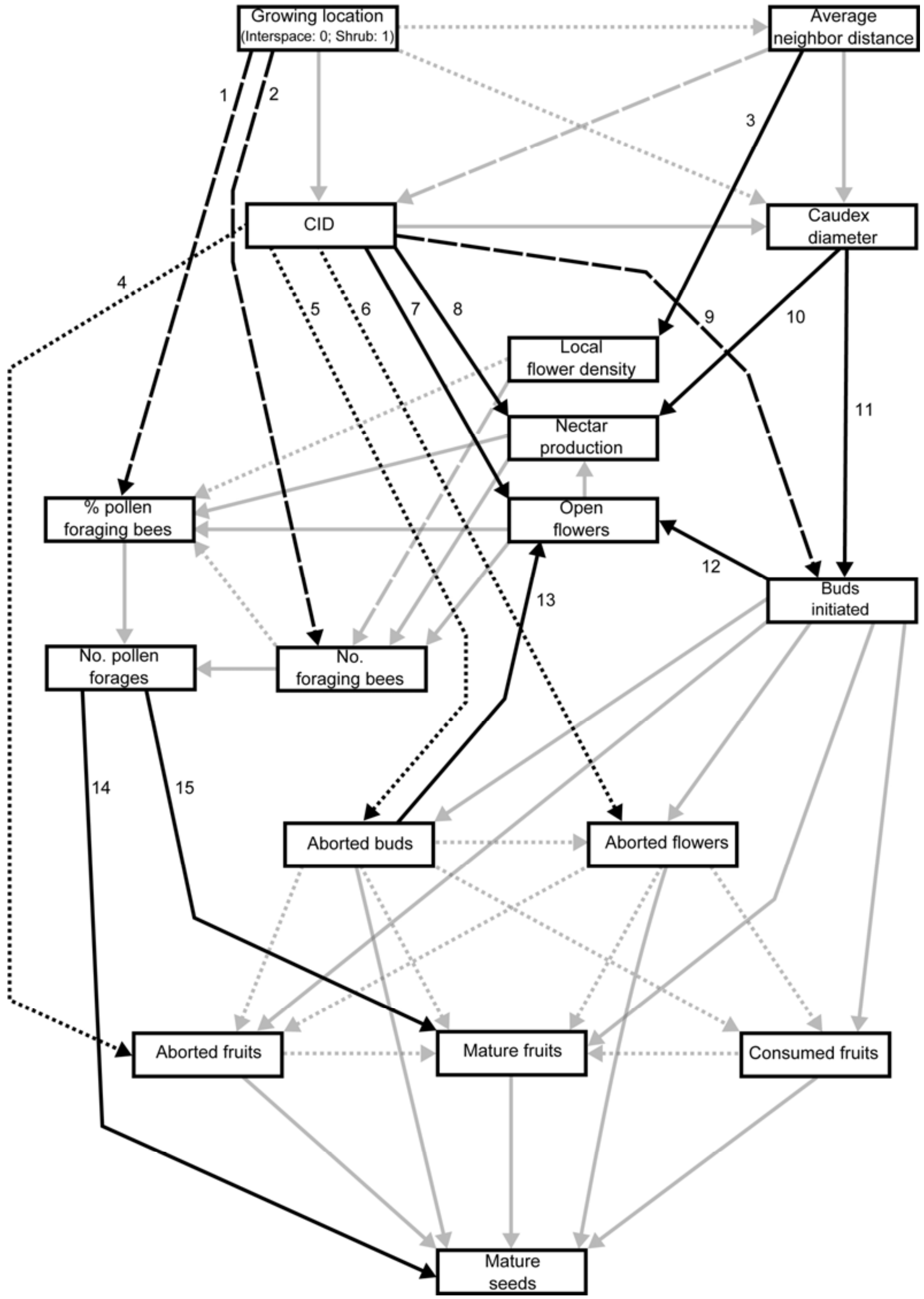

Fig. 4-2: Hypothesized causal relationships between sub-models. Black arrows show expected causal relationships between variables in different sub-models while gray arrows show relationships within sub-models (see Fig. 4-1). Dotted or solid arrows indicate expected negative or positive relationships, respectively, while dashed lines indicate the possibility of either. Theoretical justifications for each pathway is explained in the methods section (also see Appendix B).

model explores plant-pollinator interactions to determine how floral display size, nectar production, and local flower density related to pollinator foraging behavior. The final sub-model examines the reproductive ecology of individual *P. palmeri* by tracking the fate of buds as they develop into flowers and fruits, eventually producing seeds; alternatively others could be aborted during bud, flower, or fruit stages. Finally, the full model was created by allowing the three thinned sub-models to influence each other (Fig. 4-2). Modification indices (MI's) were examined to ensure that potentially important pathways that can be theoretically justified were included. Pathways that were removed were then individually added back to ensure they remain insignificant in the newly thinned model with MI's. Theoretical support for each pathway is tabulated in Appendix B.

The software package AMOS was used to produce estimates using maximum likelihood (ML), bootstrapping (BS), and Bayesian (B) approaches; these estimates are compared throughout. Maximum likelihood estimates of regression coefficients (β_{ML}) assume that data follow a continuous and multivariate normal distribution. Violation of this assumption does not affect parameter estimates, but instead results in underestimation of standard errors (SE_{ML}) resulting in increased probability of type 1 error; researchers may reject the null hypothesis, concluding that the model deviates significantly from the data, when in fact it fits the data well (see Grace 2006; Kaplan 2009).

AMOS tests multivariate normality using Mardia's coefficient of multivariate kurtosis ('*M*'; Mardia 1970, 1974) and its critical ratio (c.r.); a c.r. that exceed ±1.96 indicates a violation of multivariate normality. Although transformations can be used to help datasets follow a multivariate normal distribution, they may not completely normalize some datasets. When the assumption of multivariate normality cannot be met, bootstrapping provides a solution to both overestimated goodness of fit and underestimated parameter estimate significance. Two kinds of bootstrapping are used: Monte Carlo bootstrapping was used for parameter estimates since it allows for estimates of standard errors (SE_{BS}), and therefore probability tests (P_{BS}), without an assumption that the data match any distribution whereas Bollen-Stine bootstrapped estimates were used for overall model significance (Bollen and Stine 1992) to correct for distributional violations (reviewed in Grace 2006). A Bayesian approach was also taken to estimate regression weights (β_B) and standard errors (SE_B) and a credible interval (CI); if the CI includes zero, then the parameter estimate is deemed no different than zero. A Bayesian approach may be more appropriate for small sample datasets and non-linear relationships, but the associated pitfalls for Bayesian estimate are poorly studied (Grace 2006).

Since SEM also requires complete datasets , i.e. no missing measurements, multiple imputation (Proc MI; SAS 9.2; SAS Institute Inc. 2008) was used to estimate CID values for three missing tissue samples from one shrub and two interspace-associated plants. These were assumed to be missing at random, an assumption that is necessary for imputation and justifiable given that their absence was due to human error rather than due to an ecological process. Ten datasets were generated, each containing different estimates of CID values. The values of each estimate were averaged and substituted for missing values throughout the analysis.

Sub-model 1: plant-plant interactions

This sub-model allows for intraspecific interactions between *P. palmeri* plants and interspecific interactions between *P. palmeri* and shrubs to influence CID and plant size of *P. palmeri*. Growing location (i.e. microhabitat) was coded '0' for interspaces and '1' for shrubs. Since a previous study at the site (Chapter 2) showed that under shrubs *P. palmeri* survival is improved and their densities greater than in interspaces, growing location in the model was thought to directly influence the average distance to its nearest three conspecific neighbors (Fig.

4-1, Path 1; *Avg. neighbor dist. ← Location*). Shrubs may compete with or facilitate growth of understory plants (Miriti 2006), so location was also allowed to influence caudex diameter (Fig. 4-1, Path 2; *Caudex diameter ← Location*). Because growing under shrubs can reduce water stress in deserts (Maestre et al. 2003; Gómez-Aparicio et al. 2004), location was allowed to influence CID of *P. palmeri* (Fig. 4-1, Path 4; *CID ← Location*). Neighbor distance can indicate the degree of intraspecific interactions (Weiner 1982; Silander and Pacala 1985; Larrea-Alcázar and Soriano 2006), so average neighbor distance was allowed to influence caudex diameter (Fig. 4-1, Path 5; *Caudex diameter ← Avg. neighbor dist.*) and CID (Fig. 4-1, Path 3; *CID ← Avg. neighbor dist.*). Water stress hinders plant growth (Hsiao et al. 1976), so CID was allowed to influence caudex diameter (Fig. 4-1, Path 6; *Caudex diameter ← CID*). Two degrees of freedom were obtained by fixing the variance of the growing location parameter to 0.25 and the mean to 0.5; this is a direct result of study design, since half of the plants are under shrubs and half are in interspaces (see Appendix C for a detailed derivation of mean and variance).

Sub-model 2: plant-pollinator interactions

The aim of this sub-model is to characterize the relative importance of local *P. palmeri* flower density, per flower nectar production, and individual flower number in predicting behavior of pollinators (how many bees visited and what they would forage for while there). Since the most common visiting bees (>99%) foraged for nectar without contacting anthers or the stigma and pollen transfer by these bees probably only occurs when they actively collect pollen, total pollen forages can be influenced by two behaviors: the number (No.) of foraging bees (for nectar, pollen, or both) (Fig. 4-1, Path 16; *No. pollen forages ← No. foraging bees*) and the percentage of bees that foraged for pollen (Fig. 4-1, Path 11; *No. pollen forages ← % pollen foraging bees*). Further, pollen is a shared resource, so if more bees are foraging a smaller percentage may choose to forage for pollen (Thomson et al. 1987) (Fig. 4-1, Path 12; *% pollen foraging bees ← No.*

foraging bees), indirectly reducing the total number of times pollen was foraged for (Fig. 4-1 Path 12 & Path 11 combined).

Pollinators can be drawn to plants via visual cues (Galen 1999) and olfactory cues from nectar volatiles (Howell and Alarcón 2007). The strength of the cues from the target plant relative to its neighbors can alter foraging behavior resulting in competition for or facilitation of pollinator visitation (Rathcke 1983; Moeller 2004; Ghazoul 2006). In general, plants with flowers that produce high volumes of nectar are foraged upon more intensely (Zimmermann 1988).Thus, the number of foraging bees was allowed to respond to the number of local (1.5 m radius) conspecific flowers (Fig. 4-1, Path 13; *No. foraging bees ← Local flower density*), nectar production per flower (Fig. 4-1, Path 14; *No. foraging bees ← Nectar production*), and the number of open flowers (Fig. 4-1, Path 15; *No. foraging bees ← Open flowers*).

Small desert bees are especially susceptible to water stress and nectar can be the only water source aside from that generated metabolically (Willmer 1997). Beyond attracting bees, nectar sugar also provides bees with resources necessary for foraging activities (Willmer 1997), including pollen foraging; thus, an increased percentage of pollen foraging bees is expected on plants that have many open flowers (Fig. 4-1, Path 9; *% pollen foraging bees ← Open flowers*) and with more nectar production (Fig. 4-1, Path 8; *% pollen foraging bees ← Nectar production*). It is unclear how local flower density might influence the on-plant pollinator behavior , but the possibility that local flower density influence the percentage of bees choosing to forage for pollen is considered (Fig. 4-1, Path 7; *% pollen foraging bees ← Local flower density*). Lastly, the number of open flowers and the nectar produced per flower can be negatively correlated (reviewed in Zimmermann 1988) (Fig. 4-1, Path 10), probably because nectar is costly to produce (e.g. Southwick et al. 1981) and flowers on individual plants compete for resources (Stephenson 1981; Lee 1988).

Sub-model 3: reproductive ecology

This sub-model describes the fate of buds from bud to flower to fruit to seed. Reproduction starts with the initiation of buds and ultimately ends with seed production. Plants demonstrate complex resource allocation behaviors, often selectively aborting developing buds, flowers, fruits, and/or seeds; resources from aborted reproductive parts can then be translocated to other developing plant parts (reviewed in Stephenson 1981). Because of this within-plant competition for resources, plants that initiate more buds might be expected to abort more buds (Fig. 4-1, Path 17; *Aborted buds ← Buds initiated*), fruits (Fig. 4-1, Path 18; *Aborted fruits ← Buds initiated*) and flowers (Fig. 4-1, Path 19; *Aborted flowers ← Buds initiated*) because each competes for resources. However, plants initiating many buds should logically mature many fruits (Stephenson 1981) (Fig. 4-1, Path 20; *Mature fruits ← Buds initiated*). Further, with more fruits available more fruits are expected to be consumed (Fig. 4-1, Path 21; *Consumed fruits ← Buds initiated*) simply by virtue of having more reproductive nodes.

If resources become limited, plants can conserve them by translocating them from aborted organs to more developed; further, the cost of aborting poorly developed organs is less than aborting well developed organs (Stephenson 1981). Thus, plants with many aborted buds may have fewer aborted flowers (Fig. 4-1, Path 22; *Aborted flowers ← Aborted buds*) or fruits (Fig. 4-1, Path 25; *Aborted fruits ← Aborted buds*). Similarly, plants with many aborted flowers may have fewer aborted fruits (Fig. 4-1, Path 23; *Aborted fruits ← Aborted flowers*). The number of consumed fruits may be lower if plants aborted many buds (Fig. 4-1, Path 24; *Consumed fruits ← Aborted buds*) or flowers (Fig. 4-1, Path 28; *Consumed fruits ← Aborted flowers*) simply because there were fewer fruits to be consumed. For the same reason, the number of mature fruits may be negatively affected by the abortion of buds (Fig. 4-1, Path 26; *Mature fruits ← Aborted buds*), flowers (Fig. 4-1, Path 27; *Mature fruits ← Aborted flowers*), and fruits (Fig. 4-1, Path 29;

Mature fruits ← Aborted fruits) and fruit consumption (Fig. 4-1, Path 30; *Mature fruits ← Consumed fruits*).

The number of mature seeds may be increased by bud (Fig. 4-1, Path 32; *Mature seeds ← Aborted buds*), flower (Fig. 4-1, Path 34; *Mature seeds ← Aborted flowers*), and fruit abortion (Fig. 4-1, Path 31; *Mature seeds ← Aborted fruits*) since resources can be translocated from aborted organs to mature more seeds in remaining fruits (Stephenson 1981). Since fruits contain many seeds, plants with more mature fruits likely have more seeds (Fig. 4-1, Path 33; *Mature seeds ← Mature fruits*) and plants with more consumed fruits potentially have fewer seeds (Fig. 4-1, Path 35; *Mature seeds ← Consumed fruits*).

Full model with linked sub-models

The extent to which pollinator behavior might be directly influenced by shrubs is unclear since I did not find studies that relate benefactors to pollinator behavior. Two activities were compared for bees foraging under shrubs versus between them: the number of bees that forage for either nectar or pollen (Fig. 4-2, Path 2; *No. foraging bees ← Location*) and the percentage that forage for pollen (Fig. 4-2, Path 1; *% pollen foraging bees ← Location*). It is reasonable to predict that shrubs may directly reduce the number of foraging bees on *P. palmeri* by obscuring the visibility flowers, or by competing for or facilitating generalist pollinators via shared floral display (Rathcke 1983; Ghazoul 2006). Once a pollinator has arrived, it may choose to forage for pollen, nectar, or both. Shade under shrubs may alter behavior when desert bees face high temperatures. Bees may avoid direct sunlight when faced with overheating (Linsley 1978) so they may prefer to collect pollen from plants shaded by shrub canopies.

Shrubs were thought to indirectly influence pollinator behavior in several ways. First, shrubs can improve survival, and therefore density, of conspecific flowering *P. palmeri* (Chapter 2), so neighborhood flowering density may be higher under shrubs (Fig. 4-2, Path 3; *Local flower* *density* ← *Avg. neighbor dist.*). In turn, plants may face greater competitive or facilitative effects of neighbors on foraging activity. Second, any influence of shrubs on plant size may indirectly influence pollinator behavior since plant size can be an important determinant of nectar production (Fig. 4-2, Path 10; *Nectar production* ← *Caudex diameter*) and bud initiation (Fig. 4-2, Path 11; *Buds initiated* ← *Caudex diameter*). The latter effect is important, as plants that initiate more buds are likely to have more open flowers (Fig. 4-2, Path 12; *Open flowers* ← *Buds initiated*) and pollinators are attracted to larger display size (Galen 2005). Third, indirect relationships between shrubs and pollination may occur if shrubs influence water stress, sometimes a limiting factor to nectar production (e.g. Carroll et al. 2001; Petanidou and Smets 1996; see Galen 2005; Petanidou 2007 for review), potentially altering foraging patterns (Fig. 4-2, Path 8; *Nectar production* ← *CID*). Additionally, water stress may reduce the number of open flowers directly (Fig. 4-2, Path 7; *Open flowers* ← *CID*) since water limitation leads to flower closure and curtailed flower longevity (Galen 2005). The number of open flowers could also be limited through stress-related bud abortion since an aborted bud cannot become an open flower (Fig. 4-2, Path 13; *Open flowers* ← *Aborted buds*). It is unclear how water stress might influence bud initiation (Fig. 4-2, Path 9; *Buds initiated* ← *CID*) (reviewed in Karlsson and Méndez 2005); studies of the response of reproductive allocation to water stress are rare for perennial forbs in semi-arid environments (but see Jaksić and Montenegro 1979; more stress led to higher allocation to reproduction). If reproduction is limited by pollinators, any of these alterations of pollinator behavior by shrubs may influence the number of mature fruits or seeds, since pollination intensity can depend on floral display size (Galen 1999) and nectar reward (Zimmermann 1988) and often contributes to the number of mature seeds (Fig. 4-2, Path 14; *Mature seeds* ← *No. pollen forages*) and/or fruits (Fig. 4-2, Path 15; *Mature fruits* ← *No. pollen forages*) (reviewed in Lee 1988).

Aside from pollinator mediated effects, shrubs may alter reproduction in other ways. A reduction of water stress may directly reduce abortion of buds (Fig. 4-2, Path 5; *Aborted buds* ←

CID), flowers (Fig. 4-2, Path 6; *Aborted flowers* ← *CID*), and fruits (Fig. 4-2, Path 4; *Aborted fruits* ← *CID*) leading to indirect improvements in fruit maturation. Independent of water stress, any difference in plant size that results from growing under shrubs is expected to affect reproductive allocation (Weiner et al. 2009).

Assessment of spurious correlations

Spurious correlations can arise due to mathematical dependency between the covariate and response in regression based models like SEM; thus a portion of the observed correlation (R^2) may not be 'real' (Mitchell 1994; Brett 2004). Since the variable "total bud initiation" was formed from the sum of the possible floral fates (aborted buds, flowers, and fruits, consumed fruits, and aborted fruits), pathways leading from total bud initiation to each fate are not independent, making them prone to spurious correlation (reviewed in Brett 2004). Five pathways (Fig. 4-1, Paths 17 (*Aborted buds* ← *Buds initiated*), 18 (*Aborted fruits* ← *Buds initiated*), 19 (*Aborted flowers* ← *Buds initiated*), 20 (*Mature fruits* ← *Buds initiated*), and 21 (*Consumed fruits* ← *Buds initiated*)) were subject to spurious correlations. These potentially spurious correlations were assessed following the method described by Brett (2004), the magnitude of the spurious coefficient of determination (R^2) was estimated and percentile confidence intervals were produced (SAS 9.2; SAS Institute Inc. 2008); if the coefficient from a regression of the data used for the SEM (R^2_{SEM}) is greater than the upper confidence interval of the spurious coefficient (R^2_{SP}), then the remaining portion of the correlation is expected to be 'real'.

IV. Results

Sample means, standard deviations, correlations, units, and the transformations used for each measured variable are reported in Table 4-1. Whole plant seed production ranged from 0 to 5695 seeds for interspace-associated plants and from 0 to 2544 seeds for shrub-associated plants with a mean of 434. The top five seed producers grew in interspaces. Five plants failed to produce any seeds; four of these were interspace-associated. Results are summarized first by describing which pathways were thinned or retained (see Table 4-2) followed by a synthetic summary of the final ‘linked’ model.

Transformation reduced Mardia’s multivariate kurtosis (*M*) for the final model from 33 to 23, dropping the critical ratio (c.r.) from 4.78 to 3.28. However, since the c.r. is above the critical-limit of 1.96, the data still violate the assumption of multivariate normality after transformation. Two plants growing in interspaces appeared to be outliers; no bees were observed visiting either plant, and one produced zero seeds while the other only produced three seeds. Nonetheless, these outliers were retained because sample size is extremely limited and they represent real observations containing relevant information. These violations spurred the necessity of significance tests using Bayesian and bootstrapped estimates. Bootstrapping can be an effective measure for reliable inference when data are non-normal while Bayesian methods are useful when sample sizes are small (Grace 2006). Bootstrapped estimation also allows AMOS to estimate significance tests for any parameter estimate, including matrices for direct, indirect, and total effects. It should be recognized that bootstrapping estimates standard error (SE_{BS}) and significance tests (P_{BS}), not regression coefficients (β). Bayesian pathway estimates (β_B), standard errors (SE_B), and significance tests (pathway is significant when the range between the upper and lower 95% credible interval does not contain zero) are only provided for the final, thinned model (Table 4-3). The consistency among estimates and significance tests produced using each method indicates robustness.

Table 4-1

Variable transformations, units, means, standard deviations (SD), covariances (upper triangle) and correlations (lower triangle) of sampled *P. palmeri.*

	Location	Caudex diameter ($\sqrt[3]{\text{mm}}$)	CID (‰)	Buds initiated ($\sqrt[4]{\text{no.}}$)	Aborted buds ($\sqrt{\text{no.}}$)	Open flowers (Log_{10}(no.))	Nectar production ($\sqrt{\mu\text{L}}$)	% pollen foraging bees ($\sqrt[3]{\%}$)	No. foraging bees ($\sqrt[3]{\text{no.}}$)	No. pollen forages ($\sqrt[3]{\text{no.}}$)	Aborted fruits ($\sqrt{\text{no.}}$)	Consumed fruits ($\sqrt{\text{no.}}$)	Aborted flowers ($\sqrt{\text{no.}}$)	Avg. neighbor dist. (Log_{10}(cm))	Fruits matured ($\sqrt{\text{no.}}$)	Local flower density (Log_{10}(No.))	Seeds matured ($\sqrt{\text{no.}}$)
Location		-0.09	0.26	-0.07	-0.40	-0.01	-0.03	0.13	-0.05	0.01	-0.15	0.03	-0.25	-0.04	-0.13	0.16	-0.83
Caudex dia.	-0.49		-0.10	0.13	0.41	0.07	0.06	0.02	0.23	0.14	0.26	0.18	0.36	0.03	0.52	-0.10	2.28
CID	0.59	-0.29		-0.16	-0.76	-0.05	0.09	0.07	-0.14	-0.01	-0.36	0.07	-0.51	-0.10	-0.41	0.23	-01.7
Buds initiated	-0.23	0.59	-0.30		1.05	0.22	0.03	0.21	0.54	0.38	0.48	0.50	1.16	0.06	1.53	-0.23	7.84
Aborted Buds	-0.38	0.53	-0.40	0.84		0.55	0.04	0.31	1.36	0.80	1.42	1.00	3.34	0.19	4.02	-0.80	21.16
Open flowers	-0.04	0.44	-0.13	0.80	0.58		0.05	0.31	0.54	0.41	0.28	0.26	0.67	0.05	1.09	-0.12	5.73
Nectar production	-0.10	0.25	0.14	0.07	0.03	0.16		0.17	0.25	0.21	0.06	0.27	-0.13	0.01	0.32	0.24	1.89
% pollen foraging bees	0.23	0.06	0.07	0.30	0.13	0.59	0.22		0.82	0.95	0.22	0.39	0.59	0.04	1.24	-0.07	6.62
No. foraging bees	-0.08	0.48	-0.12	0.69	0.50	0.91	0.28	0.55		1.19	0.73	0.69	1.60	0.11	2.65	-0.23	14.17
No. pollen forages	0.01	0.36	-0.01	0.60	0.37	0.86	0.30	0.80	0.88		0.43	0.52	1.13	0.08	2.10	-0.16	11.44
Aborted fruits	-0.22	0.53	-0.30	0.60	0.51	0.45	0.06	0.15	0.42	0.31		0.68	1.52	0.12	1.40	-0.66	4.86
Consumed fruits	0.04	0.31	0.05	0.53	0.31	0.36	0.25	0.22	0.34	0.33	0.33		1.30	0.11	1.45	-0.17	7.16
Aborted flowers	-0.23	0.47	-0.27	0.91	0.75	0.69	-0.09	0.24	0.58	0.51	0.54	0.40		0.22	4.54	-1.01	20.35
Avg. neighbor dist.	-0.25	0.26	-0.32	0.29	0.26	0.30	0.04	0.10	0.24	0.21	0.27	0.20	0.30		0.15	-.37	0.12
Fruits matured	-0.09	0.48	-0.15	0.86	0.65	0.80	0.16	0.37	0.69	0.68	0.35	0.31	0.72	0.15		-.42	46.73
Local flower density	0.21	-0.19	0.17	-0.26	-0.26	-0.18	0.24	-0.04	-0.12	-0.11	-0.33	-0.07	-0.32	-0.70	-0.10		0.57
Seeds matured	-0.09	0.35	-0.11	0.73	0.57	0.70	0.15	0.32	0.61	0.62	0.21	0.26	0.54	0.02	0.88	0.02	
Mean	0.50	2.28	19.92	2.77	3.28	0.76	1.23	2.20	3.09	1.68	1.64	2.10	4.56	2.30	4.32	-0.46	23.91
SD	0.50	0.37	0.90	0.61	2.11	0.46	0.69	1.16	1.31	1.05	1.34	1.56	2.14	0.36	3.00	1.49	18.01

Note – Values are not backtransformed.

Table 4-2

Summary of the effects of pathway thinning showing the estimated effect of the pathway (β_{ML}) its standard error (SE_{ML}) and associated significance (P_{ML}), the model χ^2 with and without the pathway, the associated change in model χ^2 that results from pathway removal ($\Delta\chi^2_1$), and the overall model significance with and without the pathway. Bolded pathways were retained in the final model while others were thinned.

Pathway description						χ^2			Model significance			
									With		Without	
(Fig.-Path: Dependent var. ← Independent Var.)	β_{ML}	SE_{ML}	SE_{BS}	P_{ML}	P_{BS}	With	Without	$\Delta\chi^2_1$	P_{ML}	P_{BS}	P_{ML}	P_{BS}
Sub-model 1: plant-plant interactions												
1-6: Caudex diameter ← CID	0.016	0.061	0.059	0.797	0.884	<0.01	0.07	0.07	1.000	0.978	0.996	0.978
1-5: Caudex diameter ← Avg. neighbor dist.	0.153	0.127	0.134	0.227	0.290	0.07	1.51	1.44	0.996	0.978	0.825	0.673
1-3: CID ← Avg. neighbor Dist.	-0.456	0.285	0.260	0.109	0.170	1.51	4.01	2.50	0.825	0.673	0.548	0.401
1-1: Avg. neighbor dist. ← Location[†]	**-0.178**	**0.094**	**0.092**	**0.058**	**0.070**	**4.01**	**7.49**	**3.48**	**0.548**	**0.401**	**0.278**	**0.188**
1-2: Caudex diameter ← Location	**-0.361**	**0.088**	**0.086**	*******	**0.005**	**4.01**	**22.22**	**14.73**	**0.548**	**0.401**	**0.002**	**0.002**
1-4: CID ← Location	**1.054**	**0.199**	**0.196**	*******	**0.004**	**4.01**	**3.06**	**22.57**	**0.548**	**0.401**	*******	**0.002**
Sub-model 2: plant-pollinator interactions												
1-12: % pollen foraging bees ← No. foraging bees	-0.013	0.246	0.240	0.957	0.996	8.00	8.00	<0.01	0.156	0.325	0.238	0.395
1-13: No. foraging bees ← Local flower density	0.007	0.050	0.051	0.887	0.801	8.00	8.03	0.03	0.238	0.395	0.330	0.481
1-7: % pollen foraging bees ← Local flower density	0.030	0.090	0.095	0.742	0.799	8.03	8.13	0.10	0.330	0.481	0.421	0.523
1-8: % pollen foraging bees ← Nectar production	0.214	0.186	0.186	0.249	0.238	8. 13	9.45	1.32	0.421	0.523	0.397	0.475
1-10: Nectar production ← Open flowers	0.236	0.203	0.218	0.246	0.247	9.45	10.78	1.33	0.397	0.475	0.375	0.471
1-14: No. foraging bees ← Nectar production	**0.271**	**0.103**	**0.105**	**0.009**	**0.006**	**1.78**	**17.24**	**6.46**	**0.375**	**0.471**	**0.101**	**0.228**
1-9: % pollen foraging bees ← Open flowers	**1.466**	**0.278**	**0.323**	*******	**0.004**	**1.78**	**33.10**	**22.32**	**0.375**	**0.471**	**0.001**	**0.016**
1-11: No. pollen forages ← % pollen foraging bees	**0.408**	**0.043**	**0.054**	*******	**0.015**	**1.78**	**62.83**	**52.05**	**0.375**	**0.471**	*******	**0.002**
1-16: No. pollen forages ← No. foraging bees	**0.509**	**0.038**	**0.048**	*******	**0.008**	**1.78**	**88.75**	**77.97**	**0.375**	**0.471**	*******	**0.002**
1-15: No. foraging bees ← Open flowers	**2.514**	**0.155**	**0.173**	*******	**0.003**	**1.78**	**105.42**	**94.64**	**0.375**	**0.471**	*******	**0.002**

[†] Signifies pathways that are statistically insignificant, but were retained due to their empirical and theoretical support.

Table 4-2 continued…

Pathway description						χ^2			Model significance			
									With		Without	
(Fig.-Path: Dependent var. ← Independent var.)	β_{ML}	SE_{ML}	SE_{BS}	P_{ML}	P_{BS}	With	Without	$\Delta\chi^2_1$	P_{ML}	P_{BS}	P_{ML}	P_{BS}
Sub-model 3: reproductive ecology												
1-23: Aborted fruits ← Aborted flowers	0.005	0.162	0.195	0.976	0.971	5.39	5.39	<0.01	0.067	0.072	0.145	0.196
1-22: Aborted flowers ← Aborted buds	-0.010	0.108	0.114	0.928	0.979	5.39	5.40	0.01	0.145	0.196	0.248	0.315
1-25: Aborted fruits ← Aborted buds	0.024	0.127	0.131	0.850	0.841	5.40	5.44	0.04	0.248	0.315	0.365	0.443
1-35: Mature seeds ← Consumed fruits	0.376	0.759	0.707	0.621	0.439	5.44	5.68	0.24	0.365	0.443	0.460	0.495
1-31: Mature seeds ← Aborted fruits	-1.290	0.982	1.132	0.191	0.327	5.68	7.37	1.69	0.460	0.495	0.392	0.453
1-32: Mature seeds ← Aborted buds[††]	1.160	0.813	0.784	0.153	0.119	7.37	9.37	2.00	0.392	0.453	0.312	0.385
1-28: Consumed fruits ← Aborted flowers	-0.353	0.185	0.221	0.057	0.091	9.37	12.89	3.52	0.312	0.385	0.168	0.263
1-24: Consumed fruits ← Aborted buds	**-0.334**	**0.151**	**0.156**	**0.026**	**0.043**	**12.89**	**17.60**	**4.70**	**0.168**	**0.263**	**0.062**	**0.154**
1-34: Mature seeds ← Aborted flowers	**-1.693**	**0.753**	**0.810**	**0.025**	**0.052**	**12.89**	**17.72**	**4.83**	**0.168**	**0.263**	**0.060**	**0.170**
1-29: Mature fruits ← Aborted fruits	**-0.512**	**0.142**	**0.146**	***	**0.004**	**12.89**	**24.43**	**11.54**	**0.168**	**0.263**	**0.007**	**0.048**
1-27: Mature fruits ← Aborted flowers	**-0.639**	**0.174**	**0.228**	***	**0.012**	**12.89**	**24.93**	**12.04**	**0.168**	**0.263**	**0.005**	**0.084**
1-21: Consumed fruits ← Buds initiated	**2.336**	**0.522**	**0.526**	***	**0.008**	**12.89**	**29.86**	**16.97**	**0.168**	**0.263**	**0.001**	**0.010**
1-26: Mature fruits ← Aborted buds	**-0.525**	**0.139**	**0.148**	***	**0.009**	**12.89**	**25.56**	**12.67**	**0.168**	**0.263**	**0.004**	**0.032**
1-30: Mature fruits ← Consumed fruits	**-0.607**	**0.125**	**0.144**	***	**0.002**	**12.89**	**32.47**	**19.58**	**0.168**	**0.263**	***	**0.010**
1-18: Aborted fruits ← Buds initiated	**1.312**	**0.242**	**0.224**	***	**0.005**	**12.89**	**36.23**	**23.34**	**0.168**	**0.263**	***	**0.004**
1-20: Mature fruits ← Buds initiated	**9.277**	**0.845**	**0.103**	***	**0.005**	**12.89**	**75.71**	**62.82**	**0.168**	**0.263**	***	**0.002**
1-17: Aborted buds ← Buds initiated	**2.902**	**0.261**	**0.273**	***	**0.005**	**12.89**	**76.68**	**63.79**	**0.168**	**0.263**	***	**0.002**
1-33: Mature seeds ← Mature fruits	**6.160**	**0.537**	**0.537**	***	**0.011**	**12.89**	**79.01**	**66.12**	**0.168**	**0.263**	***	**0.002**
1-19: Aborted flowers ← Buds initiated	**3.184**	**0.205**	**0.311**	***	**0.002**	**12.89**	**103.64**	**90.75**	**0.168**	**0.263**	***	**0.002**

[††] Removal produces a modification index suggesting correlated error between seeds and fruits.

Table 4-2 continued…

Pathway description						χ^2			Model significance With		Model significance Without	
(Fig.-Path: Dependent var. ← Independent var.)	β_{ML}	SE_{ML}	SE_{BS}	P_{ML}	P_{BS}	With	Without	$\Delta\chi^2_1$	P_{ML}	P_{BS}	P_{ML}	P_{BS}
Full model with linked sub-models												
2-6: Aborted flowers ← CID	-0.007	0.145	0.166	0.961	0.876	129.36	129.37	0.01	0.040	0.597	0.047	0.617
2-14: Mature seeds ← No. pollen forages	0.719	1.445	1.424	0.619	0.440	129.37	129.61	0.24	0.047	0.617	0.052	0.625
2-2: No. foraging bees ← Location	-0.083	0.14	0.151	0.556	0.585	129.61	129.96	0.35	0.052	0.625	0.057	0.639
2-9: Buds initiated ← CID	-0.091	0.077	0.083	0.235	0.328	129.96	131.35	1.39	0.057	0.639	0.055	0.635
2-4: Aborted fruits ← CID	-0.201	0.169	0.175	0.233	0.205	131.35	132.75	1.40	0.055	0.635	0.053	0.633
2-7: Open flowers ← CID	0.035	0.045	0.053	0.434	0.534	132.75	133.36	0.61	0.053	0.633	0.056	0.637
2-8: Nectar production ← CID[†]	**0.177**	**0.104**	**0.113**	**0.088**	**0.126**	**133.36**	**136.19**	**2.83**	**0.056**	**0.637**	**0.046**	**0.611**
2-13: Open flowers ← Aborted buds	**-0.064**	**0.032**	**0.031**	**0.047**	**0.044**	**133.36**	**137.18**	**3.82**	**0.056**	**0.637**	**0.041**	**0.599**
2-1: % pollen foraging bees ← Location	**0.593**	**0.242**	**0.251**	**0.014**	**0.028**	**133.36**	**139.07**	**5.71**	**0.056**	**0.637**	**0.032**	**0.569**
2-5: Aborted buds ← CID	**-0.399**	**0.176**	**0.176**	**0.023**	**0.033**	**133.36**	**138.30**	**4.94**	**0.056**	**0.637**	**0.035**	**0.595**
2-10:Nectar production ← Caudex diameter	**0.594**	**0.253**	**0.229**	**0.019**	**0.005**	**133.36**	**138.59**	**5.23**	**0.056**	**0.637**	**0.034**	**0.575**
2-15: Mature fruits ← No. pollen forages	**0.431**	**0.187**	**0.207**	**0.021**	**0.023**	**133.36**	**138.42**	**5.06**	**0.056**	**0.637**	**0.035**	**0.593**
2-11: Buds initiated ← Caudex diameter	**0.975**	**0.182**	**0.213**	*******	**0.003**	**133.36**	**156.35**	**22.99**	**0.056**	**0.637**	**0.002**	**0.421**
2-12: Open flowers ← Buds initiated	**0.789**	**0.111**	**0.095**	*******	**0.002**	**133.36**	**168.71**	**35.35**	**0.056**	**0.637**	*******	**0.309**
2-3: Local flower density ← Avg. neighbor dist.	**-2.958**	**0.409**	**0.346**	*******	**0.004**	**133.36**	**169.75**	**36.39**	**0.056**	**0.637**	*******	**0.313**
MI1: Mature fruits ↔ Mature seeds	**-3.780**	**1.615**	**1.755**	**0.019**	**0.006**	**125.84**	**133.36**	**7.52**	**0.116**	**0.637**	**0.056**	**0.637**
MI2: Aborted flowers ↔ Nectar production	**-0.193**	**0.169**	**0.097**	**0.143**	**0.033**	**119.88**	**125.84**	**5.96**	**0.186**	**0.743**	**0.116**	**0.689**
MI3: Local flower density ↔ Nectar production [††]	0.247	0.097	0.092	0.011	0.004	111.91	119.88	7.97	0.328	0.808	0.186	0.637

[†] Signifies pathways that are statistically insignificant, but were retained due to their empirical and theoretical support.

[††] Pathway removed despite being significant since the two are not expected to related.

Table 4-3

Summary of unstandardized regression weights (β) and P-values (P) for the final model (Fig. 4-3). Subscripts correspond to the method used to derive the value: 'ML' for 'maximum likelihood', 'BS' for 'bootstrapping', and 'B' for Bayesian. For Bayesian estimates, effects are significantly different from zero when 95% credible intervals (CI) exclude zero. Bold values indicate significance tests that are discrepant in their interpretation based on an $\alpha = 0.05$ rejection level. Note: '***' = '< 0.001'

							95% Bayesian CI	
Dependent variable		Independent variable	β_{ML}	β_{B}	P_{ML}	P_{BS}	Lower	Upper
Caudex diameter	←	Location	-0.361	-0.363	***	0.008	-0.544	-0.185
CID	←	Location	1.054	1.050	***	0.005	0.638	1.465
Buds initiated	←	Caudex diameter	0.975	0.985	***	0.005	0.611	1.366
Aborted buds	←	Buds initiated	2.726	2.730	***	0.007	2.197	3.262
Aborted buds	←	CID	-0.399	-0.397	0.023	0.030	-0.757	-0.029
Nectar Production	←	CID	0.162	0.161	0.098	0.079	-0.045	0.363
Open flowers	←	Aborted buds	-0.064	-0.064	**0.047**	**0.075**	**-0.130**	**0.003**
Nectar Production	←	Caudex diameter	0.491	0.489	**0.047**	**0.049**	**-0.041**	**1.017**
Open flowers	←	Buds initiated	0.789	0.786	***	0.005	0.557	1.013
No. foraging bees	←	Nectar Production	0.271	0.271	0.009	0.016	0.053	0.490
% pollen foraging bees	←	Open flowers	1.494	1.499	***	0.003	0.949	2.042
No. foraging bees	←	Open flowers	2.514	2.519	***	0.005	2.192	2.848
% pollen foraging bees	←	Location	0.593	0.603	0.014	0.025	0.104	1.118
Aborted fruits	←	Buds initiated	1.312	1.324	***	0.004	0.814	1.831
Consumed Fruits	←	Buds initiated	2.336	2.327	***	0.006	1.229	3.415
Consumed Fruits	←	Aborted buds	-0.334	-0.334	0.026	0.039	-0.642	-0.017
No. pollen forages	←	No. foraging bees	0.509	0.510	***	0.004	0.429	0.589
No. pollen forages	←	% pollen foraging bees	0.408	0.406	***	0.004	0.316	0.495
Aborted flowers	←	Buds initiated	3.171	3.181	***	0.004	2.763	3.600
Mature fruits	←	Aborted fruits	-0.545	-0.540	***	0.004	-0.810	-0.259
Mature fruits	←	Consumed Fruits	-0.544	-0.559	***	0.005	-0.800	-0.305
Avg. neighbor dist.	←	Location	-0.178	-0.180	0.058	0.091	-0.377	0.012
Mature fruits	←	Buds initiated	8.111	8.150	***	0.004	6.247	10.139
Mature fruits	←	Aborted flowers	-0.582	-0.585	***	0.003	-0.948	-0.239
Mature fruits	←	Aborted buds	-0.348	-0.354	0.008	0.023	-0.660	-0.059
Mature fruits	←	No. pollen forages	0.418	0.410	0.014	0.023	0.037	0.784
Mature seeds	←	Aborted flowers	-2.571	-2.502	0.002	0.005	-4.289	-0.789
Mature seeds	←	Mature fruits	7.029	6.955	***	0.005	5.636	8.347
Local flower density	←	Avg. neighbor dist.	-2.958	-2.945	***	0.005	-3.784	-2.110
e14	↔	e5	-0.190	-0.223	0.024	0.017	-0.478	-0.023
e20	↔	e16	-3.690	-4.256	0.015	0.006	-8.744	-0.829

Sub-model 1: plant-plant interactions

The assumption of multivariate normality was met for this sub-model (*M* = -3.28; c.r. = -1.74). However, to maintain consistency with other sub-models, bootstrapped standard error estimates and *P*-values are still reported (Table 4-2). Initially the model fit the data perfectly ($\Delta\chi^2_2 = 0.00$, $P_{\mathrm{ML}} = 1.000$, $P_{\mathrm{BS}} = 0.978$), indicating over fitting. Three pathways were removed (Fig. 4-1; Paths: 3 (*CID ← Avg. neighbor dist.*) 5 (*Caudex diameter ← Avg. neighbor dist.*) and 6 (*Caudex diameter ← CID*)) since they did not contribute significantly to overall model fit and had insignificant regression coefficients (Table 4-2). Two pathways were not thinned (Fig. 4-1, Paths 2 (*Caudex diameter ← Location*) and 4 (*CID ← Location*)) since they greatly improved model fit and their effects were significant (Table 4-2). One path (Fig. 4-1, Path 1; A*vg. neighbor dist. ← Location*) had insignificant effects ($\Delta\chi^2_1 = 3.48$, $P_{\mathrm{ML}} = 0.070$, $P_{\mathrm{BS}} = 0.070$), but was retained since it is empirically supported by other studies (Chapter 2). The resulting thinned sub-model fit the data ($\chi^2_5 = 4.01$, $P_{\mathrm{ML}} = 0.548$, $P_{\mathrm{BS}} = 0.401$). There were negligible differences between standard and bootstrapped estimates (Table 4-2). No modification indices were reported by AMOS at any thinning step.

Sub-model 2: plant-pollinator interactions

Slight deviation from multivariate normality was detected in this sub-model (*M* = 5.36; c.r. = 2.01). The unthinned sub-model fit the data ($\chi^2_5 = 8.00$, $P_{\mathrm{ML}} = 0.156$, $P_{\mathrm{BS}} = 0.325$). However, five paths were removed (Fig. 4-1, Paths 7 *(% pollen foraging bees ← Local flower density*), 8 (*% pollen foraging bees ← Nectar production*), 10 (*Nectar production ← Open flowers*), 12 (*%pollen foraging bees ← No. foraging bees*), and 13 (*No. foraging bees ← Local flower density*)) since their regression weights were statistically indistinguishable from zero and they did not contribute significantly to overall model fit (Table 4-2). The remaining five paths (Fig. 4-1, Paths 9 (*% pollen foraging bees ← Open flowers*), 11 (*No. pollen forages ← % pollen foraging bees*), 14 (*No. foraging bees ← Nectar Production*),15 (*No. foraging bees ← Open flowers*), and 16 (*No. pollen forages ← No. foraging bees*)) were highly significant and contributed significantly to overall model-fit (Table 4-2). After thinning, the sub-model still fit the data (χ^2_{10} = 10.892, P_{ML} = 0.390, P_{BS} = 0.513). Despite slight deviation from multivariate normality, using bootstrapped estimates to make thinning decisions produces the same reduced model. No MI's were reported at any stage of thinning.

Sub-model 3: reproductive ecology

Despite transformations, the assumption of multivariate normality was still violated (*M* = 14.97; c.r. = 4.899). The unthinned model fit the data (χ^2_2 = 5.39; *P* = 0.072), but lacked parsimony (df = 2). Seven paths (Fig. 4-1, Paths 22 (*Aborted flowers ← Aborted buds*), 23 (*Aborted fruits ← Aborted flowers*), 25 (*Aborted fruits ← Aborted buds*), 28 (*Consumed fruits ← Aborted flowers*), 31 (*Mature seeds ← Aborted fruits*), 32 (*Mature seeds ← Aborted buds*), and 35 (*Mature seeds ← Consumed fruits*)) were thinned since their effects were not significantly different from zero (i.e. $P > 0.05$) and they did not contribute to overall model fit (i.e. $\Delta\chi^2_1 < 3.84$) (Table 4-1). The remaining paths (Fig. 4-1, Paths 17 (*Aborted buds ← Buds initiated*), 18 (*Aborted fruits ← Buds initiated*), 19 (*Aborted flowers ← Buds initiated*), 20 (*Mature fruits ← Buds initiated*), 21 (*Consumed fruits ← Buds initiated*), 24 (*Consumed fruits ← Aborted buds*), 26, (*Mature fruits ← Aborted buds*) 27 (*Mature fruits ← Aborted flowers*), 30 (*Mature fruits ← Consumed fruits*), 33 (*Mature seeds ← Mature fruits*), 34 (*Mature seeds ← Aborted flowers*)) were retained since their effects differed significantly from zero and contributed significantly to overall model fit (Table 4-2). After thinning the model still fit the data (χ^2_9 = 12.89, P_{ML} = 0.168, P_{BS} = 0.263).

There were no MI's produced by AMOS until the pathway from aborted buds to mature seeds (Fig 1. Path 32 (*Mature seeds ← Aborted buds*)) was eliminated; removal of this pathway produced an MI recommending negatively correlated error terms between mature seeds and mature fruits (Table 4-2, MI1: *Mature fruits ↔ Mature seeds*). Correlated error terms indicate a joint, unmeasured causal factor (Grace 2006), and it is not unreasonable to expect that some unmeasured factor increases fruit maturation while decreasing seed maturation, or vice-versa; e.g. resource competition between fruits and seeds. This MI could be resolved when the sub-models are linked together if a factor in sub-model 1 or 2 causes a joint effect on both seed and fruit maturation; thus, MI's were evaluated after the sub-models were linked together and thinned (see below). Using bootstrapped estimates of standard errors and their associated *P*-values did not change any thinning decisions (Table 4-1).

Full model with linked sub-models

Using thinned sub-models, but prior to thinning links between sub-models, the model did not fit the data using ML significance ($P_{\mathrm{ML}} = 0.040$), but did using Bollen-Stine bootstrapped significance ($P_{\mathrm{BS}} = 0.597$) (Table 4-2). Six pathways were eliminated (Fig. 4-2, Paths 2 (*No. foraging bees ← Location*), 4 (*Aborted fruits ← CID*), 6 (*Aborted flowers ← CID*), 7 (*Open flowers ← CID*), 9 (*Buds initiated ← CID*), and 14(*Mature seeds ← No. pollen forages*)) due to insignificant effects and contribution to overall model fit (Table 4-2). The effect of CID on mean per-flower nectar production (Fig. 4-2, Path 8 (*Nectar production ← CID*)) was not significant ($P_{\mathrm{BS}} = 0.126$) but was retained to allow water stress to have a slightly negative effect on nectar production as demonstrated in numerous studies (reviewed in Galen 2005; e.g. Carroll et al. 2001). The remaining pathways (Fig. 4-2, black pathways) were retained since their effects were significant ($P_{\mathrm{BS}} < 0.05$) and they contributed significantly to overall model fit ($\Delta\chi^2_1 > 3.84$). It should be noted that one pathway (Fig. 4-2, Path 13 (*Open flowers ← Aborted buds*)) had a statistically significant effect using maximum likelihood (P_{ML} = 0.047) but pathway removal led to no significant change in model fit ($\Delta\chi^2_1$ = 3.82), bootstrapped estimates were not significant (P_{BS} = 0.075) and Bayesian credible intervals included zero (Lower = -0.130; Upper = 0.003) (Table 4-3). Despite these inconsistencies, this pathway was retained due to its logical foundation (all else being equal, plants with more aborted buds should have fewer open flowers simply because they have fewer flowers surviving to anthesis). Another pathway (Fig. 4-2, Path 10 (*Nectar production* ← *Caudex diameter*)) showed inconsistency between significance tests; maximum likelihood and bootstrapped tests indicated significance (P_{ML} = 0.047; P_{BS} = 0.049) and the pathway contributed significantly to model fit ($\Delta\chi^2_1$ = 5.23), but Bayesian credible intervals included zero (Lower = -0.041; Upper = 1.017) (Table 4-3). This pathway was retained due to strong empirical support; plant size is tightly related to the resources available for reproduction (Stephenson 1981; reviewed in Weiner et al. 2009), and nectar production can require substantial investment of resources (e.g. Southwick et al. 1981).

Three MI's were produced by AMOS. One MI (Table 4-2, MI1: *Mature fruits* ↔ *Mature seeds*) suggested negatively correlated error between mature seeds and fruits; this correlated error pathway was justified by its statistically significant effect (P_{ML} = 0.019; P_{BS} = 0.006), significant contribution to overall model fit ($\Delta\chi^2_1$ = 7.52), and the possibility that it represents a resource trade-off between seeds and fruits, a frequent observation (reviewed in Stephenson 1981). It should be noted that both a correlated error term and a unidirectional arrow produce identical model fit, but if a unidirectional arrow can be theoretically justified, it is preferred. Another MI (Table 4-2, MI2: *Aborted flowers* ↔ *Nectar production*) suggested a negatively correlated error term between flower abortion and nectar production. This correlated error pathway was added due to its significance (P_{ML} = 0.024; P_{BS} = 0.033) and contribution to overall model fit ($\Delta\chi^2_1$ = 5.96); further, it is not inconceivable that flower abortion may be reduced and nectar production increased jointly by an unmeasured factor (e.g. favorable climatic conditions may have increased nectar production and reduced flower abortion). The last MI suggested a positive correlated error term between local flower density and mean per-flower nectar production (Table 4-2, MI3: *Local flower density ↔ Nectar production*); despite its statistical significance ($P_{\mathrm{ML}} = 0.011$, $P_{\mathrm{BS}} = 0.004$), empirical and theoretical support is lacking for this specific relationship and it was removed. After thinning sub-models and links between sub- models the final model (Fig. 4-3) fit the data ($\chi^2_{107} = 119.88$; $P_{\mathrm{ML}} = 0.186$, $P_{\mathrm{BS}} = 0.637$).

Assessment of spurious correlations

Estimated coefficients of determination from regressions of the original data (R^2_{SEM}) were all well above the upper 95th percentile of estimated expected spurious coefficients (R^2_{SP}) (Table 4-4), indicating that the majority of the coefficients of determination (R^2_{SEM}) for these pathways are not due to mathematical dependency.

Synthesis of results for the final model

It should be recognized that any suggestion of causality (e.g. X reduced Y) simply refers to the effects that were modeled, rather than true causality. Ultimately, seed production was significantly influenced by every variable in the final model except average neighbor distance, local flower density, CID, and the number of aborted buds (Table 4-5, TE's); though CID and the number of aborted flowers have multiple pathways to seed production (Fig. 4-3), these multiple pathways counter each other such that they balance to have no total effect. Plant size (caudex diameter) was a key correlate of seed production; its modeled direct positive effect on bud initiation was related to an array of cascading effects on pollination and reproduction (Fig. 4-3; Table 4-5, TE's). Larger plants also produced more nectar per flower, increasing visitation intensity ('*No. foraging bees*') (Fig. 4-3). Higher pollen foraging intensity ('*No. pollen forages*') significantly increased seed production by increasing the number of mature fruits, but bud

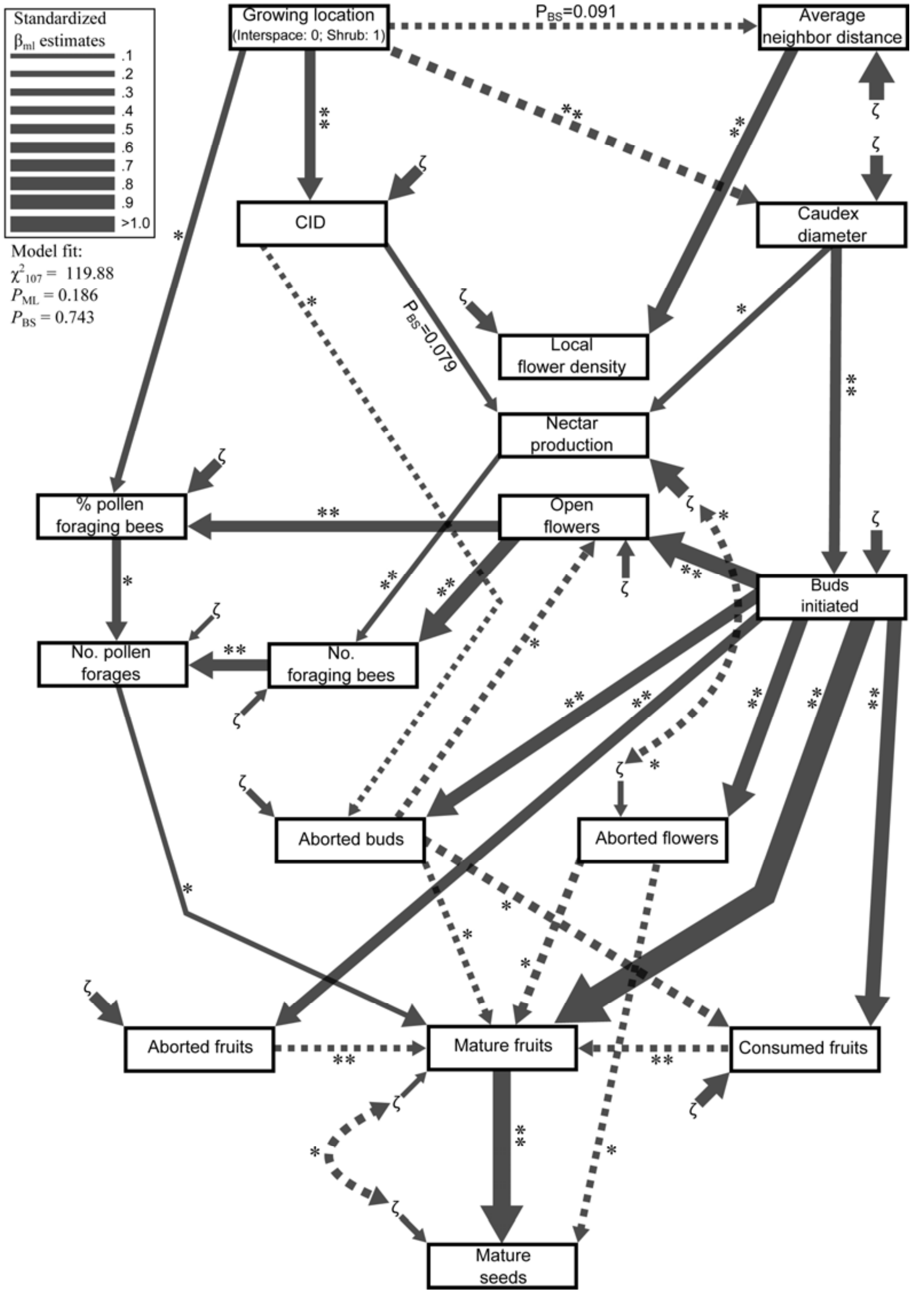

Fig. 4-3: Final SEM. Solid and dashed lines represent positive and negative relationships, respectively. Line thickness is proportional to the magnitude of relationships (see legend). Unexplained variance for each measured variable is specified by arrows labeled ‘ζ’. Single-headed arrows represent direct effects; double-headed arrows indicate correlated error. Asterisks indicate bootstrapped *P*-values (‘**’= ‘$P < 0.01$’; ‘*’ = ‘$P < 0.05$’).

Table 4-4
Comparison of the coefficient of variation from the data used for the SEM (R^2_{SEM}) and that of the estimated spurious correlation (R^2_{SP}) due to the mathematical dependency due to 'buds initiated' being derived as a sum of all five possible bud fates. Values of R^2_{SEM} are significantly larger than R^2_{SP} at the $\alpha = 0.05$ level when R^2_{SEM} is greater than the upper 5% of the percentile confidence interval (CI).

Pathway description (Fig.-Path: Dependent var. ← Independent var.)	R^2_{OD}	R^2_{SP}	Percentile CI Lower 5%	 Upper 5%
1-17: Aborted buds ← Buds initiated	0.70	0.14	0.03	0.28
1-19: Aborted flowers ← Buds initiated	0.82	0.24	0.10	0.41
1-18: Aborted fruits ← Buds initiated	0.36	0.01	<0.01	0.11
1-20: Mature fruits ← Buds initiated	0.73	0.36	0.20	0.52
1-21: Consumed fruits ← Buds initiated	0.28	0.04	<0.01	0.14

initiation was much more important (Fig. 4-3; Table 4-5, TE's). All three stages of abortion (bud, flower, and fruit) resulted in direct reductions in the number of mature fruits, but bud abortion also indirectly reduced fruit consumption, which indirectly increased fruit maturation; thus, bud abortion had a neutral effect on the number of mature fruits and seeds (Table 4-5, TE's). In addition to reducing the number of mature fruits, flower abortion also had a significant direct negative effect on the number of mature seeds (Fig. 4-3; Table 4-5, DE's). Growing location was much more important than average neighbor distance for seed production (Table 4-5, TE's). Average neighbor distance only influenced local flower density, a measure that had no significant effect on any other variables (Fig. 4-3; Table 4-5). The model explained a significant proportion of variation in each measured variable, but only a small amount of variation was explained for nectar production and average neighbor distance; the remaining variables had at least 25% of their variation explained (Table 4-5).

Three key differences were associated with growing location, each important for seed production. Plants associated with shrubs (1) had smaller caudex diameters but (2) suffered less water stress (i.e. greater CID) and (3) had a greater percentage of bees that actively foraged for pollen; neighbors appeared to be somewhat closer on average for plants under shrubs, but the

Table 4-5

Standardized direct effects (DE) (upper triangle) and total effects (TE) (lower triangle) between variables. Subtracting DE from TE yields the total indirect effects (IE). Bold values indicate statistical significance ($P_{BS} < 0.05$). Ellipses (…) represent constrained relationships where the effects are fixed at zero. Variables use the transformations shown in Fig. 4-1.

	Location	Caudex diameter	CID	Buds initiated	Aborted buds	Open flowers	Nectar production	% pollen foraging bees	No. foraging bees	No. pollen forages	Aborted fruits	Consumed fruits	Aborted flowers	Avg. neighbor distance	Fruits matured	Local flower density	Seeds matured
Location		**-0.49**	**0.59**	...	...	...	...	**0.27**	...	...	...	...	...	-0.25	...	...	...
Caudex diameter	**-0.49**		...	**0.59**	...	...	**0.27**	...	...	...	...	...	...	...	...	...	...
CID	**0.59**	...		...	**-0.17**	...	0.21	...	...	...	...	...	...	...	...	...	...
Buds initiated	**-0.29**	**0.59**	...		**0.80**	**1.03**	...	...	...	...	**0.60**	**0.90**	**0.90**	...	**1.63**	...	...
Aborted buds	**-0.34**	**0.47**	**-0.17**	**0.80**		**-0.29**	...	...	...	...	...	**-0.44**	...	...	**-0.24**	...	...
Open flowers	**-0.21**	**0.48**	0.05	**0.81**	**-0.29**		...	**0.62**	**0.89**	...	...	...	...	...	...	...	...
Nectar production	<0.01	**0.27**	0.21	...	...	...		...	**0.14**	...	...	...	...	...	...	...	...
% pollen foraging bees	0.14	**0.29**	**0.03**	**0.50**	**-0.18**	**0.62**	...		...	**0.45**	...	...	...	...	...	...	...
No. foraging bees	**-0.18**	**0.46**	**0.07**	**0.72**	**-0.25**	**0.89**	**0.14**	...		**0.65**	...	...	...	...	...	...	...
No. pollen forages	**-0.06**	**0.43**	**0.06**	**0.69**	**-0.24**	**0.85**	**0.09**	**0.45**	**0.65**		...	...	...	...	**0.14**	...	...
Aborted fruits	**-0.17**	**0.35**	...	**0.60**	...	...	...	...	...	...		...	...	...	**-0.24**	...	...
Consumed fruits	-0.12	**0.33**	**0.08**	**0.55**	**-0.44**	...	...	...	...	...	...		...	...	**-0.28**	...	...
Aborted flowers	**-0.26**	**0.54**	...	**0.90**	...	...	...	...	...	...	...	...		...	**-0.41**	...	**-0.30**
Avg. neighbor dist.	-0.25	...	...	...	...	...	...	...	...	...	...	...	...		...	**-0.70**	...
Fruits matured	**-0.22**	**0.52**	0.03	**0.87**	-0.15	**0.12**	**0.01**	**0.06**	**0.09**	**0.14**	**-0.24**	**-0.28**	**-0.41**	...		...	**1.16**
Local flower density	0.18	...	...	...	...	...	...	...	...	...	...	...	...	**-0.70**	...		...
Seeds matured	**-0.18**	**0.44**	0.03	**0.73**	-0.17	**0.14**	**0.02**	**0.07**	**0.11**	**0.16**	**-0.28**	**-0.33**	**-0.78**	...	**1.16**	...	
Variance explained (R^2)	NA	**0.243**	**0.347**	**0.352**	**0.717**	**0.662**	**0.084**	**0.382**	**0.845**	**0.912**	**0.356**	**0.350**	**0.818**	**0.064**	**0.876**	**0.497**	**0.793**

measured effect was not statistically significant (Fig. 4-3; Table 4-5, DE’s). The reduction of plant size under shrubs had a negative effect on seed production which outweighed the positive effects associated with lower water stress and increased pollen foraging behavior, resulting in a net negative effect of shrubs on seed production (Table 4-5, TE’s). Similarly, despite shrub-related direct increases in the percentage of pollen foraging bees, the small plant size of shrub associated plants resulted in lower nectar production and fewer open flowers resulting in fewer total pollen forages relative to plants growing in interspaces (Table 4-5, TE’s); however, this difference in total pollen forages would be greater if the direct positive effects of shrubs were absent.

Plants with higher CID (less water stress) aborted fewer buds (after controlling for the number of initiated buds) and had slightly higher mean per-flower nectar production; though the latter effect was statistically insignificant, but retained for its strong theoretical basis (Carroll et al. 2001; Galen 2005). Through these two modeled direct effects, water stress had a wide range of modeled indirect effects. Water stress directly increased bud abortion, reducing the number of open flowers, which was the most important factor for both the number of foraging bees and the percentage that foraged for pollen (Fig. 4-3; Table 4-5, TE’s). In contrast to bud abortion, water stress had no significant effect on flower or fruit abortion (Table 4-2). Ultimately, the effect of water stress on bud abortion did not translate to reduced seed production per plant; despite the direct negative effect of bud abortion on the number of mature fruits, plants with more aborted buds incidentally had significantly fewer consumed fruits (Table 4-5; TE’s).

Pollinators responded strongly to the number of open flowers in both the number of visiting bees and the percentage that foraged for pollen (Fig. 4-3; Table 4-5, TE’s). Nectar production was far less important; more bees visited plants with higher per flower nectar production, though their on-plant behavior was unchanged (Fig. 4-3; Table 4-5, TE’s). Bees did not appear to respond to local conspecific flower density, but, as previously mentioned, a higher percentage of bees foraged on shrub-associated *P. palmeri* Fig. 4-3; Table 4-5, DE's).

V. Discussion

Seed and fruit production in *P. palmeri* were ultimately influenced by nearly every factor hypothesized as important, supporting the notion that reproductive output is limited by many direct and indirect factors rather than any one factor (Lee 1988; Campbell and Halama 1993; Mitchell 1994). As expected, plant size the primary limiting factor for seed production during this season (2009); larger plants initiated more buds and produced more nectar per flower, consistent with previous reviews showing that plant size is an important determinant of resource availability to reproductive effort (Stephenson 1981; Bonser and Aarssen 2009; Weiner et al. 2009). After controlling for size related effects, those plants with more observed active pollen forages matured more fruits, suggesting that pollen also limits seed production in *P. palmeri*, but much less than resources. These results support other SEM studies that concluded that resources and pollen both simultaneously limit seed production (Campbell and Halama 1993). Surprisingly, water-stressed plants produced similar numbers of fruits and seeds despite having significantly higher numbers of aborted buds. However, this observation is perhaps due to local resource density dependence for fruit-consumers (see Antonovics and Levin 1980); negative effects of more aborted buds included positive effects of having fewer consumed fruits suggesting that plants demonstrating high bud abortion either had fewer fruits to consume, or, fruits had lower forage quality. The other factors that were of little importance to seed production were average neighbor distance and flowering density. Average neighbor distance had no effect, except to increase local flower density, which did not alter the number of visiting bees or the percentage that foraged for pollen.

These observations are consistent with the general hypotheses that negative and positive plant interactions occur simultaneously (Bertness and Callaway 1994; Callaway 1995; Callaway and Walker 1997; Maestre et al. 2003) and that facilitation benefits earlier ontogenetic stages more than later stages (Miriti 2006). Specific to the first hypothesis, smaller plant size under shrubs coupled with reduced water stress suggests that shrubs simultaneously compete with *P. palmeri* for some non-water resource(s) (e.g. light, nutrients) while facilitating water sufficiency. Additionally, when plants grew under shrubs, the percentage of bees that foraged for pollen was greater after accounting for the number of open flowers, but the number of foraging bees was not directly impacted, suggesting that shrubs altered the on-plant behavior of pollinators without altering visitation. When combined, the suppressive effect that the shrub association had on *P. palmeri* size outweighed the facilitative effects that shrubs had on water stress and pollen foraging activity, suggesting that resources competition with shrubs is important in limiting seed production. In contrast, the lack of a relationship between neighbor distance and either water stress or plant size suggests that intraspecific competition did not limit *P. palmeri* reproduction during this season. Regarding differences in ontogenetic sensitivity, the significant impact that water stress had on bud abortion, but not flower or fruit abortion, suggests that either buds are aborted first when water becomes limited, or, water was acutely limiting during bud formation. The latter possibility, though potentially important in some systems, is not supported, given the acropetal development of inflorescence in *P. palmeri*; a single inflorescence holds buds, flowers, and fruits simultaneously. Instead, it seems more likely that buds are ‘the first to go’ when water becomes limiting since plants have invested little water in buds relative to flowers and fruits. Such a pattern is consistent with the more general hypothesis that facilitation acts most strongly on early developmental stages (e.g. seedlings vs. adults; Miriti 2006); however, these results provide evidence that facilitation of water sufficiency scales down to benefit the least developed reproductive parts within an individual as well as the least developed individuals in a population (Chapter 2).

Foraging behavior (both the number foraging and the percentage that foraged for pollen) of bees was most strongly driven by floral display size (no. of open flowers), a pattern that has been demonstrated repeatedly (see Galen 1999), suggesting that plants with more open flowers are more desirable sources of forage to bees. Nectar production and growing location were important as well. That nectar production influenced the number of foraging bees supports studies arguing that bees can remember to return to rewarding plants (see Cartar 2004) and/or can evaluate rewards without visiting to forage (Howell and Alarcón 2007), possibilities that have previously been argued against (Zimmermann 1988). Both behaviors could optimize foraging (sensu MacArthur and Pianka 1966). The observed increase in pollen foraging behavior among shrub-associated plants may be due to altered floral micro-habitat (e.g. shade or shelter from wind). Thus, pollinators may spend less time collecting nectar for their own metabolic maintenance and more time collecting pollen to provision their offspring if they are foraging on flowers shaded by shrubs. Flowers exposed to full sun are expected to have lower relative humidity and higher temperatures, potentially altering nectar evaporation (Petanidou 2007) which could indirectly alter the foraging decisions of bees. Similarly, bees exposed to higher temperatures associated with open microhabitats may choose to forage for nectar rather than pollen since nectar can act to cool bees (Heinrich 1980a, b). Visitation rates and behavior of bees on plants were unaffected by neighborhood flowering density, suggesting that near neighbors neither compete with nor facilitate pollination services. However, because of the substantial amount of work that has shown that patch density can influence visitation rates (Rathcke 1983; Moeller 2004; Ghazoul 2006), its effects on seed production and particularly offspring fitness should continue to be considered in future studies, especially given the nearly significant effects that shrubs had on seed production.

Significant correlated error terms indicate the presence of an unmeasured joint effect on the two variables considered (Grace 2006). Negatively correlated error between the number of mature seeds and fruits suggest that a common factor increases one measure while reducing the other. Such a pattern could result from trade-offs between seed and fruit production (see Stephenson 1981). In addition, the significant negatively correlated error term between nectar production and flower abortion suggests that some unmeasured factor simultaneously increases nectar production while enhancing flower retention. This effect may be due to limitation of some unmeasured climatic or soil resource that limits nectar production and flower maturation. Regardless of the cause, the model accounts for these relationships rather than assuming their independence, resulting in stronger inference among measured factors.

Studies examining the intercorrelated effects of competition and facilitation on reproduction are lacking. By using SEM, this study demonstrates how the simultaneous direct and indirect effects of facilitation and competition on plant reproduction can be explored. This study demonstrates the potential for exploring simultaneous direct and indirect interactions between organisms within the same trophic level (plant-plant interactions) and between trophic levels (plant-pollinator interactions) using SEM. Further, SEM can be used in a multi-stage fashion, starting with an exploratory mode and shifting to a more powerful confirmatory mode as hypotheses are generated (Grace 2006). Lastly, exploratory SEM can be a useful tool for generating hypotheses that can later be subjected to experimental manipulations and for identifying which variables should be measured and controlled for.

Estimated effects of spurious correlations related to the ‘buds initiated’ variable were significantly less than the correlation detected in the unmodified data. This suggests that although spurious correlations arose due to mathematical dependency, the effects were small. The combined effects of the five spurious correlations on seed production are unclear; however, what is clear is that a large portion of the correlations are due to real variation in bud initiation. Such results highlight the importance of ensuring that observed effects are not completely driven by mathematical dependency. Methods for accounting for mathematical dependencies are lacking, but the ability to estimate their effects indicates the possibility of adjusting regression coefficients and model fit measures in SEM to remove their effects.

Care must be taken when interpreting the results of the final model. First, the exploratory approach taken does not demonstrate causality. Second, it must be recognized that the results are contingent on the model selected to interpret from and the sampling methods; there may also be many competing alternative models with equal or greater fit to the data (Grace 2006). For example, the correlated error between mature seeds and mature fruits could be replaced with a directional arrow from mature seeds to mature fruits with no consequence to model fit; doing so would imply a feedback between the number of seeds and fruits in which plants that produce many seeds could not produce as many fruits.

Outliers and violations of the assumption of multivariate normality were present, but transformations linearized most relationships, leading to substantial improvements. Small sample sizes are also of great concern, further limiting the generality of these results. Since the use of bootstrapped estimates significance and Bayesian estimates of parameters did not alter the conclusions reached, except for conflicting statistical inference regarding two pathways (*Open flowers ← Aborted buds* and *Nectar production ← Caudex diameter*; Table 4-3), it can be concluded that the model was fairly robust despite deviation from normality and the presence of outliers. The remaining unexplained variation in fruit and seed production could be partially explained by measurement error, seed consumption, genetics, unmeasured climatic variability, and parasites, among many more factors.

Generalized statements about the observed patterns are not advised as these data are limited to a single site, species pair, and year. Longer term studies are recommended since the balance between facilitation and competition fluctuates temporally (Casper 1996; Greenlee and Callaway 1996; Tielbörger and Kadmon 2000; Maestre et al. 2003; Abdallah and Chaieb 2010; Soliveres et al. 2010) and varies over multiple spatial scales (Rayburn and Monaco 2011).

Nonetheless, incorporating facilitation into more well-studied theoretical constructs has been called for by others (Bruno et al. 2003) and the application of SEM to for this purpose is promising.

Examining plant-plant interactions, plant-pollinator interactions, and reproductive ecology in unison led to a greater understanding of the potential drivers of seed output in *P. palmeri*. The use of SEM simplified the challenge of interpreting the effects of highly correlated variables on seed production. Evaluation of direct, indirect, and total effects illuminated the relative contribution of facilitation and competition for seed production. Using an exploratory mode of SEM, theoretical constructs that have historically been treated separately were studied in unison; however, a confirmatory approach is required to validate the generality of these correlative patterns in other locations, times, and species pairs. These results should spur other researchers interested in the role of facilitation on reproduction to consider the influence of altered microhabitat on the behavior of pollinators. Understanding the role of plant-plant interactions, especially positive interactions, in the reproductive fitness of plants deserves further attention.

VI. References

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CHAPTER 5

CONCLUSION

In the Wildland Urban Interface (WUI) (sensu Radeloff et al. 2005) of the Spring Mountains National Recreation Area (SMNRA) land managers face the challenge of managing hazardous fire fuel loads near human populations, infrastructure, and wildfire escape corridors while simultaneously preserving the habitat of species covered under the Clark County Multiple Species Habitat Conservation Plan (MSHCP) covered species (RECON 2000). A variety of mechanical methods are to be used to manage fuel loads, including thinning of woody species (see Ostoja et al. 2010) that are likely to facilitate other species (Gómez-Aparicio 2009). Facilitation can be an important component of species habitat since it can geographically expand the beneficiaries realized niche space by ameliorating extreme conditions at niche boundaries (Bruno et al. 2003). Thus, if woody species facilitate MSHCP covered plant species, or plant species that are larval or nectar host plants for MSHCP covered butterflies, their removal could constitute a loss of habitat. In general, fuel load reduction within the WUI is increasingly accomplished mechanically (e.g. whole tree/shrub removal) that attempt to mimic prescribed fire (Kalabokidisl and Philip 1998). However, there is little understanding of how MSCHP covered species might respond to these treatments (Ostoja et al. 2010).

Here, I synthesize the empirical findings of chapters 2-4 and discusses their implications for ecological theory and land management policy; specifically, I argue that an understanding of plant-plant interactions in the WUI can help land managers balance the objectives of reducing fuel loads to protect human populations and infrastructure while minimizing loss of habitat for desirable species. The general focus is to describe the effects of shrubs on *Penstemon palmeri* performance over many life-stages. While *P. palmeri* is not directly covered under the MSHCP, it is of interest since it is a nectar host plant for adults of the endemic Spring Mountains checkerspot butterfly (*Chlosyne acastas robusta*) (reviewed in: Ostoja et al. 2010; Pinyon Environmental Engineering Resources Inc. 2011). However, since *C. acastus* use a diversity of species for nectar, any findings of positive or negative impacts of shrubs on *P. palmeri* do not demonstrate significant impacts on *C. acastus* populations. Additionally, most of this research is at the scale of individual *P. palmeri,* rather than their populations, making it ill advised to extrapolate these finding to the population level. Further, these study sites may be below the habitable elevation of *C. acastus* (Pinyon Environmental Engineering Resources Inc. 2011). Nonetheless, these results provide valuable insight into the influence of shrubs throughout the life-cycle of *P. palmeri* and add to our theoretical understanding of the importance of shrubs in this arid ecosystem.

The major objectives of this thesis were to: (1) describe interspecific spatial associations over several years between shrubs and *P. palmeri* (Chapter 2); (2) evaluate the effects of shrub association on the performance of individual *P. palmeri* plants (Chapters 2-4); (3) use a factorial experiment to disentangle the above ground effects of *Artemisia tridentata* canopies on seedling emergence and seedling survival from the effects of the soils that accumulate beneath canopies (Chapter 2); and (4) use SEM to examine the direct and indirect effects of the shrub *Eriodictyon angustifolium* on *P. palmeri* seed and fruit production (Chapter 4). The final objective, addressed in this chapter, is to discuss the theoretical and policy implications of these results for the management of species covered under the Clark County MSHCP in the areas of the Spring Mountains National Recreation Area that have been mechanically thinned.

Theoretical implications

Ecologists are increasingly recognizing that both positive and negative plant-plant interactions can be important driving forces for structure and function of plant communities (reviewed in Brooker et al. 2008; Brooker and Callaway 2009). Facilitation can increase productivity and diversity across entire regions (Pugnaire and Lázaro 2000) and allows species to expand their realized niches into environments that would otherwise be considered inhospitable (Bruno et al. 2003).

The studies in this thesis suggest that at these sites, shrubs facilitate the survival of smaller and younger *P.palmeri* and improve bud-to-fruit maturation success, but shrubs also appear to suppress *P. palmeri* emergence, delay their reproductive initiation, and reduce their growth rates (Chapter 2). Further, experimental evidence suggests that it is the soils beneath shrub canopies that reduce emergence rates and increase survival, while the shrub canopy effects appear to be much less important (Chapter 3). The results of chapters 2 and 3 add to the growing number of studies demonstrating life-stage conflicts (Schupp 2007) and ontogenetic shifts of plant interactions from facilitative at earlier life stages (e.g. survival) to competitive at later life stages (e.g. growth and reproduction) (Miriti 2006; Schiffers and Tielborger 2006; Gómez-Aparicio 2009; Soliveres et al. 2010). These two chapters provide observational and experimental evidence that shrubs, primarily their associated soils, alter the nature of seed-seedling conflicts in a ways that may promote persistence of *P. palmeri* in the seed bank, as well as the resistance and resilience of their populations to environmental perturbations (discussed in Chapter 3). Additionally, by describing spatial associations between *P. palmeri* populations and shrubs across multiple censuses, Chapter 2 provided suggestive evidence that facilitation of seedling survival shifts spatial patterns from associative to dissociative; highlighting the importance of including a temporal component when studying spatial patterns (reviewed in Lepš 1990).

While the effects of competition on plant reproduction are well documented (Weiner 1988), studies reported in Chapters 2 and 4 add to the relatively few number of studies examining the potential facilitation of reproduction (e.g. Casper 1996; Shumway 2000; Tielbörger and Kadmon 2000; Choler et al. 2001; Kikvidze et al. 2001; Tirado and Pugnaire 2003; Griffith 2010; Soliveres et al. 2010; Cranston et al. 2012); however, few of these studies accounted for plant size in their models (reviewed in Chapter 2) and none examined the potential for shrubs to alter the behavior of pollinators visiting the plants in their understory (see Chapter 4). More importantly, Chapter 4 demonstrates how SEM can be used to identify the factors that limit reproduction in plants and incorporate facilitation into theoretical frameworks that have historically focused only on competition.

Land Management Policy Implications

Understanding plant interactions can improve our ability to posit new ways to conserve and restore the habitat of MSHCP covered species. Successful conservation and restoration requires an understanding of desirable species habitat availability and suitability. An understanding of interactions between plants can greatly improve our ability to manage vegetation in a way that maximizes the habitat area for a desirable species. Restoration ecologists have traditionally relied on removal of undesirable species in order to eliminate competition with desirable species, but they are increasingly using woody plants as facilitators in order to promote establishment of desirable species (Gómez-Aparicio 2009). However, the existence of facilitation does not always mean it will be useful for restoration activities; the utility of the facilitator for restoration depends on the beneficiary life-stage, which performance metrics are improved, and the environmental context of plant interactions (King and Stanton 2008).

Balancing the objectives of fuel load management near human populations with the objectives of conservation plans can be aided by an understanding of how plants interact in their community. Specific to the SMNRA, MSHCP covered plant species and plants used by MSHCP covered butterflies as larval and nectar hosts (desirable species) may aggregate with the woody fuels being removed. Aggregated patterns sometimes indicate a history of facilitative interactions (Fowler 1986; Callaway 2007; Brooker et al. 2008) so if desirable species demonstrate this pattern, land managers should be wary of removing their neighbors. Experiments should be conducted to assess the effect of removal on the performance of desirable species; ideally, these should include assessments of interactions at every life stage for a complete understanding of the demographic impact of removal. In areas where desirable species benefit from removal, management of fuels may serve a double benefit; removal reduced fuel loads and increases the habitable space of desirable species. Caution must be taken, however, since invasive species may also benefit from the removal (e.g. Griffith 2010), especially if conditions allow for rapid uptake of nutrients that may remain in the soil long after removal (see Bechtold and Inouye 2007). If removal improves desirable species emergence, but not their survival (a seed-seedling conflict; sensu Schupp 1995), then removal may deplete the seed-bank as many seedlings emerge, but most die before contributing to the next generation. If removal has the opposite effect, seedling emergence is improved by shrubs but seedling survival is hindered, then removal should be selectively used only after emerged seedlings are well established, and only if removal has lasting positive effects on reproduction.

Future directions for further research

Many MSHCP plant species were not covered in these investigations. Similar associative patterns have been observed between shrubs and a population of *Eriogonum umbellatum*, the sole larval host plant for the MSHCP covered Spring Mountains dark blue butterfly (*Euphilotes ancilla purpurea*) (reviewed in Ostoja et al. 2010; Pinyon Environmental Engineering Resources Inc. 2011). Patterns of association were detected between *E. umbellatum* at the lower elevations of Lee Canyon, but no further investigations were made (Poulos, unpublished data); based on these associative patterns, considering interactions between shrubs and this important larval host plant may allow land managers to assess the effect of removal on this critical larval host plant.

Chapter 2 was limited in its ability to determine the causes of spatial association between *P. palmeri* populations and shrubs; however, factorial studies (e.g. Chapter 3) and structural equation modeling (e.g. Chapter 4) were particularly useful in resolving those limitations.

Understanding the causes of spatial dissociation between emerged seedlings and shrubs (Chapter 2) can be achieved by using seed sowing experiments (e.g. Chapter 3) and investigating the distribution of *P. palmeri* populations in the seed bank using greenhouse studies of soil samples (e.g. Carrillo-Garcia et al. 2000). Further, caging experiments may prove useful in understanding the role of seed and seedling predators and herbivores in altering the spatial distribution of *P. palmeri* populations. Finally, these observations occurred over a relatively short duration and focus on post-emergence life-stages which limits our ability to understand the complete role of shrubs in *P. palmeri* life-history, especially the seed dispersal, survival, and germination stages; future studies could benefit greatly by contrasting the entire fate of *P. palmeri* individuals in shrub and interspace microhabitats, from seed to reproductive adult. Future studies should compare the soil characteristics of interspaces to those accumulated under *A. tridentata* to help understand why this shrub's soil was associated with reduced seedling emergence, but improved survival relative to interspace soils (Chapter 3). Further attention needs to be given to testing whether the stages of the seed-seedling conflicts that are improved or worsened are different between interspace and shrub microhabitats; long term studies and simulations could be particularly useful to assess how seed-seedling conflicts might influence seed bank persistence and a plant population's resistance and resilience to environmental perturbations. Demographic models (e.g. Griffith 2010) would be particularly useful for translating individual-level shrub effects to the scale of populations and confirmatory SEM's could test the generality of the SEM developed in Chapter 4 (or similar SEM's) in new areas and with new species.

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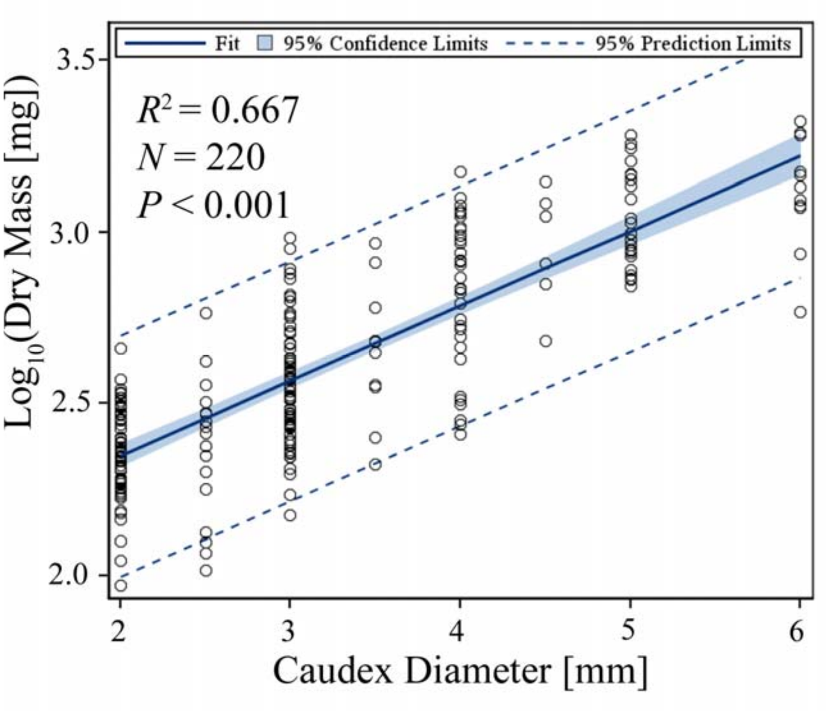
APPENDICES

Appendix A. Size-Biomass curve



Appendix A: Size (caudex diameter; mm) regressed on the logarithm of biomass (dry aboveground mass; mg). Data arise from 220 destructively sampled, greenhouse reared *P. palmeri* seedlings (taken from Poulos et al. in manuscript).

Appendix B. Pathway descriptions and the potential mechanisms and processes responsible for their possible effects. Path numbers refer to the paths found in Figs. 4-1 and 4-2.

	Fig.-Path	Description	Possible mechanism(s)/process(es)
Sub-model 1: plant-plant interactions	1-1	Growing location → Avg. neighbor dist.	Facilitation of seedling and adult survival leads to closer neighbors (Chapter 2).
	1-2	Growing location → Caudex diameter	Competition with shrubs may reduce growth leading to smaller size (Miriti 2006).
	1-3	Avg. neighbor dist.→ CID	Plants with further neighbors may face lower intraspecific competition (Weiner 1982) for water or may have water facilitated by hydraulic redistribution (reviewed in Ryel 2004).
	1-4	Growing location → CID	Shrubs can ameliorate water stress of plants growing beneath them (Maestre et al. 2003; Gómez-Aparicio et al. 2004).
	1-5	Avg. neighbor dist.→ Plant size	Intra-specific competition is partially a function of neighbor distance (Weiner 1982; Silander and Pacala 1985).
	1-6	Water stress → Plant size	Growth is particularly sensitive to water-stress (Hsiao et al 1976); thus water stress may result in reduced plant size.
Sub-model 2: plant-pollinator interactions	1-7	Local flower density → % pollen foraging bees	If surrounded by many flowers, pollinators may choose to leave for flowers on more rewarding plants since they may forage optimally (MacArthur and Pianka 1966).
	1-8	Nectar production → % of pollen foraging bees	Rewarding plants are often foraged upon more intensely (Zimmermann 1988) and nectar provides energy for other tasks, like foraging for pollen.
	1-9	Number of open flowers → percentage of pollen foraging bees	Bees often focus foraging effort on plants with many flowers (Galen 1999).
	1-10	Number of open flowers → nectar production	Flowers may compete for limited resources (Stephenson 1981) leading to lower per flower nectar production (reviewed in Zimmermann 1988).
Sub-model 2: plant-pollinator interactions cont….	1-11	Percentage of pollen foraging bees → No. pollen forages	A higher percentage of pollen foraging bees implies that a plant will receive more pollen forages.
	1-12	No. foraging bees → percentage that forage for pollen	Pollen is a shared resource, so if more bees are foraging a smaller percentage may choose to forage for pollen (Thomson et al. 1987).
	1-13	Local flower density → number of foraging bees	Plants in dense flower patches may be visited more or less due to facilitation and competition for pollinator services (Rathcke 1983; Moeller 2004; Ghazoul 2006).
	1-14	Nectar production → number of foraging bees	Bees may remember rewarding plants (Pyke 1978) and/or detect nectar volatiles (Howell and Alarcón 2007) leading bees to focus foraging efforts on plants with higher nectar production than their neighbors.
	1-15	open flowers → number of foraging bees	Plants with many flowers draw in more bees leading to an increase in the number of foraging bees (reviewed in Galen 1999).

	1-16	No. foraging bees → No. pollen forages	Plants that have many foraging bees are more likely to have their pollen foraged upon.
Sub-model 3: reproductive ecology	1-17	Bud initiation → aborted buds	Plants that initiate more buds are expected to abort more buds, flowers, and fruits, have more mature and consumed fruits simply because there are more bud fates being followed.
	1-18	Bud initiation → aborted fruits	
	1-19	Bud initiation → aborted flowers	
	1-20	Bud initiation → mature fruits	
	1-21	Bud initiation → consumed fruits	
	1-22	Aborted buds → aborted flowers	Translocation of resources from aborted buds to developing flowers may reduce the flower abortion (Stephenson 1981).
	1-23	Aborted flowers → aborted fruits	Translocation of resources from aborted flowers to developing fruits may reduce fruit abortion (Stephenson 1981).
Sub-model 3: reproductive ecology cont…	1-24	Aborted buds → consumed fruits	Plants that aborted fewer buds may have fewer fruits consumed since buds did not survive long enough to be eaten.
	1-25	Aborted buds → aborted fruits	Translocated resources from aborted buds to developing fruits may reduce fruit abortion (Stephenson 1981).
	1-26	Aborted buds → mature fruits	Plants that abort more buds may mature fewer fruits since fewer buds survived.
	1-27	Aborted flowers → mature fruits	Plants that abort more flowers may mature fewer fruits since fewer flowers survived.
	1-28	Aborted flowers → consumed fruits	Plants that aborted more flowers should implicitly have fewer fruits consumed since flowers died before being eaten.
	1-29	Aborted fruits → mature fruits	Plants that aborted fewer fruits may have fewer fruits matured since flowers died before maturation was complete.
	1-30	Consumed fruits → mature fruits	Plants with many consumed fruits may have fewer fruits matured since fruits were consumed before maturation.
	1-31	Aborted fruits → mature seeds	Resources may be translocated from aborted fruits or buds to increase the number of mature seeds (Stephenson 1981).
	1-32	Aborted buds → mature seeds	
	1-33	Mature fruits → mature seeds	Plants with more mature fruits should implicitly have more mature seeds since fruits contain seeds.
	1-34	Aborted flowers → mature seeds	Resources may be translocated from aborted flowers to increase the number of mature seeds (Stephenson 1981).

	1-35	Consumed fruits → mature seeds	Plants with many consumed fruits may have fewer seeds matured since fruits were consumed before maturation.
Linked model	2-1	Growing location → percentage of pollen foraging bees	Altered microhabitat by shrubs may modify pollinator behavior on plant; a higher or lower percentage of bees may collect pollen due to either a shade effect on pollinator thermoregulation (Linsley 1978), or indirect alteration of nectar or pollen production.
	2-2	Growing location → number of foraging bees	Shrubs may visibly obscure flowers (novel hypothesis) or compete for shared pollinators, reducing the number of foraging bees; shrubs may also facilitate pollination through shared floral display (Rathcke 1983; Gazhoul 2006).
	2-3	Neighbor distance → local flower density	Plants with distant neighbors should intrinsically have lower local flower density.
	2-4	Water stress → aborted fruits	Plants under water stress may have more aborted fruits (Saavedra et al. 2003; Wubs et al. 2009).
	2-5	Water stress → aborted buds	Plants under water stress may have more aborted buds (e.g. Saavedra et al. 2003; reviewed in Galen 2005).
	2-6	Water stress → aborted flowers	Plants under water stress may have more aborted flowers (Saavedra et al. 2003; Wubs et al. 2009).
	2-7	Water stress → open flowers	Water limitation during flowering may lead to flower closure and reduced longevity (Galen 2005).
	2-8	Water stress → nectar production	Water limitation may reduce nectar production (reviewed in Galen 2005; e.g. Carroll et al. 2001).
	2-9	Water stress → buds initiated	Plants may allocate different amounts of resources to reproduction in response to water limitation (Karlsson and Méndez 2005).
	2-10	Caudex diameter → nectar production	Larger plants may have increased per-flower nectar production since plant size is closely related to the resources available to reproduction (Stephenson 1981; reviewed in Weiner et al. 2009) and provisioning nectar requires a substantial amount of photosynthate (e.g. Southwick 1984).
	2-11	Caudex diameter → buds initiated	Larger plants may initiate more buds since the amount of resources available through translocation as well as the ability to obtain more resources through roots and leaves are tightly related to plant size (Stephenson 1981).
Linked model cont…	2-12	Buds initiated → open flowers	Plants that initiate more buds should have more open flowers simply because more had the chance to develop.
	2-13	Aborted buds → no. of open flowers	Plants with many aborted buds may have fewer flowers open simply because less survived to anthesis.

	2-14	No. pollen forages → mature seeds	Pollination intensity is often positively related to the number seeds developed per fruit (reviewed in Lee 1988), thus highly foraged plants may have produce more seeds after controlling for fruit number.
	2-15	No. pollen forages → mature fruits	Additional foragers may promote fruit growth and development since pollen tube growth stimulates the transition to fruiting (reviewed in Lee 1988).

Appendix C. Derivation of mean and variance for the 'growing location' parameter.

The growing location parameter consists of twenty-seven 0's representing 'interspace' associated plants and twenty-seven 1's representing 'shrub' associated plants. Therefore sample size (N) = 54. Given the data, we know that

$$\sum_{i=1}^{N} X_i = \sum_{i=1}^{N} X_i^2 = 27,$$

where X_i = the ith observed value.

And since

$$\text{Mean} = \mu = \frac{1}{N}\sum_{i=1}^{N} X_i \text{ , so}$$

$$\mu = 27/54 = 0.5.$$

To calculate variance we know:

$$\text{Variance} = \sigma^2 = \frac{1}{N}\sum_{i=1}^{N} X_i^2 - \mu^2\text{, so}$$

$$\sigma^2 = 27/54 - (0.5)^2 = 0.25$$