

Mechanisms for maintenance of dominance in a nonclonal desert shrub

STANLEY G. KITCHEN,[†] SUSAN E. MEYER, AND STEPHANIE L. CARLSON

*United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory,
Provo, Utah 84606 USA*

Citation: Kitchen, S. G., S. E. Meyer, and S. L. Carlson. 2015. Mechanisms for maintenance of dominance in a nonclonal desert shrub. *Ecosphere* 6(12):252. <http://dx.doi.org/10.1890/ES15-00083.1>

Abstract. Blackbrush (*Coleogyne ramosissima*: Rosaceae) is a slow-growing, non-clonal shrub that is regionally dominant on xeric, shallow soils in the North American Mojave Desert–Great Basin transition zone and southern Colorado Plateau. Blackbrush seed production is concentrated in mast years, and most seeds are cached and later consumed by heteromyid rodents. Vegetation histories show that blackbrush stands can persist apparently unchanged for over a century. We used dendrochronological techniques to examine plant age distributions, recruitment patterns and growth rates, to ascertain how blackbrush achieves this long-term population stability. Our study addressed the following questions: (1) What is the role of within-clump recruitment in long-term patterns of clump persistence? Do blackbrush clumps accrue new cohorts through time? (2) How does recruitment vary temporally, specifically in relation to years of mast seed production and climate variability? (3) What impact does intra-specific competition have on plant growth rates? To address these questions, we aged stems from 208 clumps in five Mojave Desert and four Colorado Plateau populations. Individual plant age estimates ranged from 3 to 122 years. Clumps comprised of multiple-aged cohorts were ubiquitous. Within clumps, plant and cohort number increased with clump age, suggesting a steady accumulation of new cohorts over time. Clumps in Colorado Plateau populations accumulated cohorts at a significantly faster rate than clumps in Mojave Desert populations. Recruitment occurred in relatively frequent pulses. It was only partially synchronized with mast years, with some seedling establishment following years of low seed production. Individuals that recruited into established clumps averaged half the radial growth rate of individuals that recruited into openings. Blackbrush recruitment is bimodal, with initial colonization of open spaces from rodent caches but with long-term clump persistence a product of periodic, within-clump recruitment of new plants. This dual recruitment strategy provides a mechanism for continued community dominance in an abiotically stressful environment under low levels of disturbance.

Key words: age structure; blackbrush; *Coleogyne ramosissima*; Colorado Plateau; dendrochronology; growth rate; life-history strategies; masting; Mojave Desert; seedling bank; stress tolerance.

Received 13 February 2015; revised 6 July 2015; accepted 7 July 2015; **published** 8 December 2015. Corresponding Editor: E. Ribbens.

Copyright: © 2015 Kitchen et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

[†] **E-mail:** skitchen@fs.fed.us

INTRODUCTION

It has long been recognized that plant community dynamics are strongly influenced by the life history strategies of the component species

and that life history strategies in turn are shaped by environmental factors related to abiotic stress and disturbance regimes (Grime 1977). Species long-term success and persistence in a plant community can best be described as full self-

replacement through time, implying the operation of life-history traits that provide a balance between costs and potential benefits of traits essential for individual longevity and new recruitment (Silvertown and Charlesworth 2001). On the other hand, the capacity to occupy and dominate a plant community over time is a measure of success that goes beyond basic self-replacement. Dominance can be defined in terms of total biomass or resource capture capacity relative to the community as a whole (Whittaker 1965). Plant communities in which ecosystem processes perpetuate existing patterns of dominance can be considered stable. Conversely, processes which alter ecosystems to the extent that dominant species become poorly adapted reduce community stability. Thus, knowledge of adaptive strategies that enable species to achieve and maintain dominance is needed to predict plant community stability in response to change. Life-history strategies that enable a species to first effectively occupy a large proportion of available space and second, to hold that space once occupied through ongoing self-replacement, should facilitate community dominance.

In xeric environments, dominant shrub species must be resilient to extremes in the physical environment and associated abiotic stresses. They are expected to exhibit strategies for stress tolerance that feature slow growth, late maturity, and long life span (Grime 1977). Life-history traits that result in infrequent recruitment while maintaining community dominance are also often associated with long-lived shrubs in warm deserts (Ackerman 1979, McAuliffe 1988, Hunter 1989, Cody 2000). Individual plant longevity, and thus stand stability, is often maintained through such mechanisms as vegetative regeneration or clonal expansion (e.g., creosote bush (*Larrea tridentata* (DC.) Coville; McAuliffe et al. 2007).

Blackbrush (*Coleogyne ramosissima* Torrey: Rosaceae) is a desert shrub that is often dominant where it occurs, frequently forming near-monocultures on shallow soils in areas transitional between cold and warm deserts of western North America (Bowns and West 1976, West 1983, Callison and Brotherson 1985, Meyer and Pendleton 2005). Some features of blackbrush life history fit the paradigm for a stress-tolerant dominant species while others appear contradictory. Blackbrush is slow-growing and apparently

long-lived, forming stable populations that have been shown to persist for centuries (Webb et al. 1987, 2011). Its leaves are microphyllous and facultatively deciduous (Bowns 1973, Ackerman and Bamberg 1974, Ackerman et al. 1980), stress-resistance adaptations enabling plant survival through multiple cycles of drought (Smith et al. 2004). Unlike many stress-tolerant desert shrubs, however, blackbrush regularly produces large seed crops and appears to have generally high investment in sexual reproduction, with estimated seed yields as high as 300 kg ha⁻¹ in high-production years (S. Meyer, *unpublished data*). Production of the moderately large seeds (one-seeded achenes; mean mass $\approx$ 17 mg; Pendleton 2008) is limited primarily to mast years, especially at drier sites (Pendleton et al. 1995; Meyer and Pendleton 2015a). Masting, defined as ‘the synchronous intermittent production of large seed crops by perennial plants’ (Kelly and Sork 2002) has rarely been reported for desert shrubs. It is commonly associated with the need to satiate seed predators, in this case the heteromyid rodents that also disperse and scatter-hoard the seeds (Bowns and West 1976, Auger 2005, Meyer and Pendleton 2015b). Successful seedling establishment takes place primarily from rodent caches, though emergence under shrub crowns from seeds that have not undergone secondary dispersal is also possible (Meyer and Pendleton 2015b). Thus, masting validates seed predation as a selective force without masking the counterbalancing benefits of predator-assisted seed dispersal on fitness. In addition to selecting for intermittent reproduction, post-dispersal vertebrate seed predation favors reduced seed bank residence time, which can be detected as an absence or reduction in the dormancy mechanisms necessary for maintenance of persistent seed banks (Pendleton and Meyer 2004, Meyer and Pendleton 2005).

Interactions among seedling, juvenile and adult conspecifics within plant communities are dynamic and feature a combination of facilitative and competitive effects (Holmgren et al. 1997, Montgomery et al. 2010). In stressful environments, juveniles may benefit from close proximity to adults through amelioration of the abiotic environment (Brooker et al. 2008, Valladares et al. 2008). Benefits to sub-adult plants may include reductions in direct irradiance, air and

soil temperatures and vapor pressure deficit, and from increases in soil nutrients. Nurse plants may also provide protection from herbivory (McAuliffe 1986). The net outcome of competitive and facilitative interactions may be transitory, switching with ontogenetic development as maturing plants become less vulnerable to stress (Miriti 2006, Wright et al. 2014).

Blackbrush has a long history in the American desert southwest. Woodrat midden macrofossil assemblages indicate a restricted late Pleistocene distribution relative to that of the present, with records from the lowest elevations in the Grand Canyon (Cole 1990*a, b*) and along the southern Colorado River drainage (King and Van Devender 1977, Van Devender 1990), respectively hundreds of meters below or kilometers south of current distribution limits. The upward and northward expansion of blackbrush during Holocene warming (past 10,000–12,000 years; Cole 1990*b*, Coates et al. 2008) and more nuanced shifts associated with the Little Ice Age (1400–1900 CE; Hunter and McAuliffe 1994) demonstrate that the species has the capacity to migrate and adjust spatially in response to changing climate given sufficient time.

Recent studies (Richardson and Meyer 2012, Richardson et al. 2014) support recognition of two meta-populations of blackbrush. Eastern populations are found on xeric uplands on the southern Colorado Plateau (CP) while western populations occupy habitats at the upper elevational limits of the Mojave Desert (MD) creosote bush-dominated vegetation zone and are transitional to Great Basin cold-desert communities. Climate for CP ecoregion populations is generally drier than for MD ecoregion populations, with a larger relative percentage of annual precipitation associated with summer monsoons (Richardson et al. 2014). Winter temperatures are substantially colder on the CP than MD, with less extreme differences in mean summer temperatures.

In this study, we employed dendrochronological techniques to evaluate plant age distributions among and within clumps, reconstruct recruitment histories and assess variation in growth rates for MD and CP populations of blackbrush. These techniques were first developed for trees (Stokes and Smiley 1968), but dendrochronological methods can also be applied to shrubs and

even herbaceous plants if appropriate protocols are employed (Schweingruber and Poschold 2005). Interest in shrub dendrochronology has increased rapidly in recent years, especially for alpine and arctic ecosystems experiencing shrub invasion related to global warming (Myers-Smith et al. 2015). Recent studies on shrubs of arid and semi-arid ecosystems are less common (e.g., Milton et al. 1997, Seligman and Zelman 2000, Poore et al. 2009, Srur and Villalba 2009, Olano et al. 2011, Eugenio et al. 2012, Génova et al. 2013). The utility of this approach for understanding the population biology of desert shrubs is clear, however, from both these recent studies and earlier studies (e.g., Roughton 1972, Cawker 1980).

A limitation in dendrochronological studies of many desert shrubs, including blackbrush, is their tendency to crown-split with age, precluding the possibility of precise aging of older individuals (e.g., Milton et al. 1997). Crown-splitting is thought to be an adaptation to drought that reduces the effects of cavitation and allows different sectors of a shrub genet to independently exploit soil microenvironments that may differ in water availability (Lambert et al. 2011). It is not a form of clonal expansion, but instead is an adaptation that may increase the longevity of a genet by reducing the probability of drought-induced mortality.

Study objectives

The goal of the present study was to examine individual plant ages and recruitment histories of blackbrush populations representing the MD and CP meta-populations to address the following questions: (1) What is the role of within-clump recruitment in long-term patterns of clump persistence? Do blackbrush clumps accrue new cohorts through time? (2) How does recruitment vary temporally, specifically in relation to years of mast seed production and climate variability? (3) What impact does intra-specific competition have on plant growth rates? We were also interested in whether these patterns would differ for populations in the MD vs. CP ecoregions.

METHODS

Field sampling

We measured clump maximum height, widest

Table 1. Study site location, clump sampling intensity by size class (sdlg = seedling/postseedling; juv = juvenile/pre-adult; and mat = full adult/mature) and age data for mature blackbrush clumps taken from nine study sites.

Ecoregion and site name	Latitude (North)	Longitude (West)	Elev. (m)	Clumps sampled			Dates for oldest wood in mature clumps	
				sdlg	juv	mat	Mean	Range
Mojave Desert								
Beaver Dam Summit	37°06'01"	113°49'20"	1484	7	5	10	1923	1906–1942
Toquerville Turnoff	37°16'48"	113°18'41"	1164	16	24	20	1972	1943–1985
Veyo Road	37°16'24"	113°38'38"	1423	5	5	10	1930	1885–1963
Winchester Hills	37°13'25"	113°37'54"	1227	5	5	10	1952	1923–1979
La Grande	37°10'33"	113°20'19"	985	0	0	10	1949	1911–1990
Colorado Plateau								
N. of Hanksville	38°47'36"	110°26'12"	1343	7	5	10	1973	1951–1990
Dirty Devil Turnoff	38°09'35"	110°37'15"	1500	8	5	10	1953	1918–1982
Little Rockies	37°45'36"	110°39'06"	1700	8	5	10	1952	1916–1979
Gemini Bridges	38°39'34"	109°40'47"	1393	0	0	8	1963	1922–1994

crown diameter and crown diameter perpendicular to widest diameter, and then destructively sampled 208 blackbrush clumps from five MD and four CP blackbrush-dominated communities (Table 1). Clumps were defined as one or more stems arranged with a more or less common center giving the appearance of shared identity (Fig. 1A). Multiple stems in a clump may be

physically connected (i.e., sharing common roots) or separate. Multi-stemmed clumps result from: (1) crown-splitting of individual plants, (2) synchronous establishment of multi-plant cohorts from rodent-cached seed (Fig. 1B), (3) asynchronous establishment of individuals or multi-individual cohorts within the clump over time (Fig. 1C, D), or (4) any combination of these

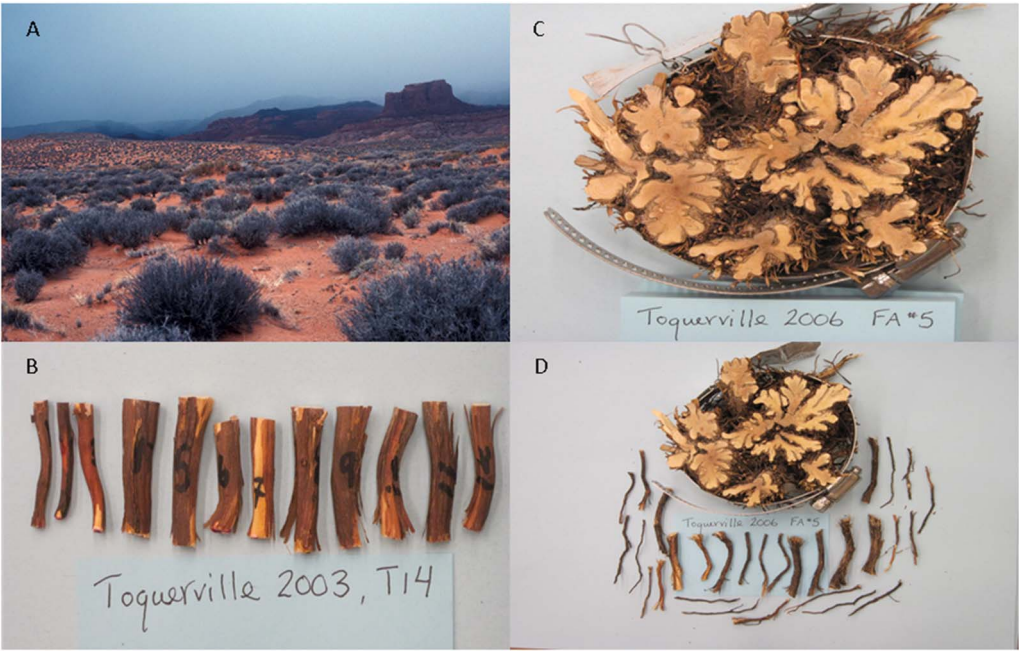


Fig. 1. Mature blackbrush clumps in a natural setting (A); a series of 12 separate cross-cut stems (plants) from one clump dated to the same year (single cohort; B); cross-cut of a multi-plant clump held together with hose clamp before (C) and after (D) smaller stems were removed.

Table 2. Pooled demographic analysis for pre- and post-1970 blackbrush clumps (based on the oldest dated wood) collected from five Mojave Desert and four Colorado Plateau study sites.

Ecoregion and age group	Plants per clump		Plants per cohort		Cohorts per clump		Mean cohort interval (yrs)
	Mean	Range	Mean	Range	Mean	Range	
Mojave Desert							
Post-1970	2.7	1–22	1.8	1–12	1.3	1–5	8.8
Pre-1970	6.5	1–23	1.7	1–7	3.7	1–11	12.1
Colorado Plateau							
Post-1970	4.5	1–29	1.9	1–11	1.9	1–6	6.2
Pre-1970	12.1	1–32	1.8	1–9	6.1	1–11	8.5

processes. Crown-splitting in blackbrush occurs because of the uneven way in which new xylem tissue is arranged in growth rings producing a characteristic lobed to compound-lobed symmetry (Fig. 1D). Although crown sprouting and layering are alternative mechanisms for producing multi-stem clumps in some species, these processes are not known to occur in blackbrush and were not observed in this study. The essentially universal absence of vegetative re-growth after fire-induced crown mortality provides additional indirect evidence that blackbrush lacks the capacity for vegetative regeneration.

During sampling, variable-sized, adjustable hose clamps (max. diameters 38–127 mm) were fitted around the base of most large clumps in order to hold individual stems in their approximate positions relative to other stems in the clump. Smaller hose clamps and plastic ties were used with smaller clumps when deemed prudent. Clumps were extracted by carefully digging to below the zone of principal root production, which is usually quite shallow in this species (<50 cm). Sample clumps were excavated using a spade after which roots and stems were trimmed using hand clippers. Clamps were tightened during this process, and later as needed, particularly when root and shoot removal allowed a more compact clump configuration while at the same time preserving within-clump orientation of individual stems (Fig. 1C). Trimmed samples for clumps and individual stems were labeled and bagged to conserve the plant, clump, and site identification.

Samples were collected over a 10-year period (2003–2012) with 67% (140) of clumps sampled in either 2006 or 2008. Samples were selected to include a full representation of the range in clump size present at each site. Clumps were

field-classified before sampling based upon broad size/ontogenetic categories: seedling (seedling/post-seedling; mean crown diameters 2–20 cm), juvenile (juvenile/pre-adult; mean crown diameters 15–43 cm), and full-adult/mature (mean crown diameters 37–159 cm) phases.

Laboratory protocols

Clump and individual stem samples were cross-cut to a length of 2–5 cm using a band saw with root collars visually positioned at the center-point between upper (stem) and lower (root) cut surfaces. Cut surfaces were prepared for growth-ring analysis using a belt sander and fine-grit sandpaper until cell structure and growth ring boundaries were clearly visible on individual stems and fragments with magnification (15–75×).

We cross-dated growth ring series for each stem using as markers, rings that were consistently narrow for each ecoregion and that were associated with historically dry years (Stokes and Smiley 1968). Stems with growth ring series that could not be cross-dated (<10%) were not included in further analysis. Stems within clumps were assigned to the same plant when breakage surfaces, stem shape and within-clump orientation indicated a common origin (Fig. 1C). When pith was present, the year assigned to pith was designated as the germination year. When pith was missing (due to decay or splitting), the year assigned to the oldest growth ring (OGR) from all associated stems was used to estimate minimum plant age. Similarly, the OGR in a clump was used as an estimate of minimum clump age (Table 1). A total of 1032 plants were aged with a mean of 5.0 (range 1–32) plants per clump (Table 2).

Cohort classification

Within clumps, one or more plants with a common germination year (pith date) were grouped into recruitment cohorts. Cohort germination year was determined using pith year for 93% of clumps dated to 1970 or later (post-1970 age class). The presence of datable pith for post-1970 plants growing within older clumps (pre-1970 wood present) was equally high allowing for precise determination of germination year and corresponding cohort designation for these plants. Plants without pith were more difficult to accurately group into cohorts due to the unknown and variable time lags between OGR and germination years. Thus plants without pith were arbitrarily grouped into putative cohorts allowing a maximum OGR age difference of 6 years. When these protocols were not sufficient to clearly designate a single cohort option for each plant, cohort assignment was determined by selecting the most conservative grouping scenario for each clump, that is, the grouping that resulted in the least number of cohorts. In limited testing, increases in the maximum within-cohort age difference by 1–2 years had virtually no effect on total number of cohorts per clump, suggesting stability in cohort number using this approach. A total of 513 cohorts were assigned to 208 clumps for a mean of 2.5 cohorts per clump (Table 2).

We estimated interval length for cohort sequences using the year of oldest wood for each cohort (pith or OGR) for endpoints. We differentiated cohort intervals as (1) initial interval, representing the estimated time from oldest dated wood in a clump to the oldest wood of the second cohort, and (2) secondary intervals, all inter-cohort intervals that occurred within clumps after first interval. Lengths (years) were assigned to 86 initial and 214 secondary intervals across ecoregions.

Recruitment history reconstruction

We tabulated known recruitment years based on plants with pith dates pooled for each ecoregion to obtain an estimate of recruitment frequency. Yearly recruitment between 1970 and 2005 was classified for each ecoregion as high, moderate or low based upon the comparison between the pooled yearly total and the ecoregion median for this 36-year period of record.

We also compared major recruitment years at the ecoregion level to known mast years between 1991 and 2001 (Meyer and Pendleton 2015a) and with annualized (October–September) estimates of the Palmer Drought Severity Index (PDSI) for Dixie (MD) and Southeast Utah (CP) climate divisions developed from PRISM data for the time period 1970–2005 (WWDT 2014). PDSI integrates the effects of variable atmospheric temperature and the timing and quantity of precipitation producing a reliable surrogate for soil water condition.

Growth rate determination

We calculated stem radial growth rate for 644 plants with piths dated to 1970 or later. We restricted this analysis to plants from this time period because older plants were often compound-lobed and fragmented making a simple diametric measure of growth less obtainable and less meaningful. We assumed that stem radial growth would correlate with more detailed measures of growth and would therefore suffice as a proxy for total plant growth in a general sense. Growth rate was calculated as the average annual increase in stem diameter at the root collar (mean stem diameter (mm)/plant age). We determined mean stem diameter as the average of the maximum diameter and the diameter in the direction perpendicular to the maximum.

Individual plant growth rate values were divided into three groups based on levels of intra-specific competition using the presence, number, and relative ages of companion plants. Plants that occurred singly or as members of initial (oldest in clump), low-density (2–4 plants) cohorts were combined into a low competition group. Plants that occurred as members of initial, high-density (5+ plants) cohorts were assigned a moderate competition level. We assumed that because of their much smaller size, plants belonging to secondary cohorts would not be a major source of competition for plants in initial cohorts and hence their abundance (or absence) was not used to estimate competition intensity for older, clump-initiating plants. All plants that were members of secondary cohorts (older cohorts present in the clump) were grouped into a high competition level.

We considered the possibility that plant age might confound growth rate results, especially if

plant age distributions differed among competition classes. However, mean plant ages were almost identical for low (16.2 years) and high (15.5 years) completion classes (moderate competition class 25.5 years). Age distributions were also evenly dispersed for all three groupings (data not shown). We examined the relationship between plant age and growth rate within competition classes using linear regression. R^2 values (<0.08) indicated that age was a poor predictor of growth rate and suggest that plant age had little or no impact on growth rate, at least for these relatively young plants.

Statistical analysis

We used ANCOVA (analysis of covariance; SAS 9.3 Proc GLM) to test the hypotheses that cohort number and plant number within a clump would increase with clump age (continuous variable) and that the slope of this relationship would vary by ecoregion (class variable). We also used Proc GLM to perform ANOVA (analysis of variance) to evaluate the effects of ecoregion and cohort interval class (initial or secondary) on cohort interval length and to examine the effects of ecoregion and competition level on radial growth rate.

RESULTS

Individual plant age estimates ranged from 3 to 122 years, based on pith dates for younger plants and on OGR (minimum age) for a majority of older plants. Age of mature clumps varied among sites, with youngest clumps found at the Toquerville and North Hanksville sites and oldest clumps found at the Beaver Dam Summit and Veyo Road sites (Table 1). Mean age of mature clumps varied by 50 years among MD sites and by 21 years among CP sites.

Plants and cohorts per clump

We dated the oldest wood per clump to 1970 or later for 68% of MD and 71% of CP clumps, respectively. Contrary to the expectation for seedlings emerging from rodent caches, the majority (59% MD; 52% CP) of these relatively young clumps were represented by a single plant. However, multiple-individual clumps, including clusters of 8+ plants (8% MD; 19% CP), were also common, creating a strongly

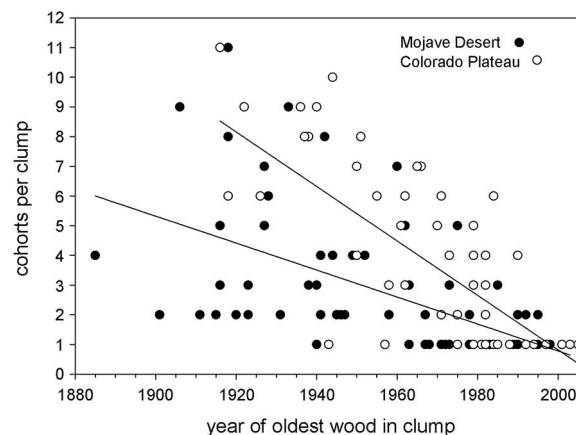


Fig. 2. Blackbrush cohorts per clump regressed against age of oldest wood in the clump for five Mojave Desert (MD) and four Colorado Plateau (CP) sites demonstrating that CP clumps acquire cohorts at a faster rate than MD sites ($P < 0.0001$).

skewed distribution for number of plants per clump for this age class (Table 2). The number of cohorts per clump was also skewed for the post-1970 age class with 1–12 plants grouped into a single cohort for 84% of MD and 70% of CP clumps, respectively. For older clumps (pre-1970 wood present), we identified multiple plants for 90% of clumps and 8+ plants for 31% of MD and 73% of CP clumps. Overall, CP clumps contained more plants than MD clumps ($F = 7.38$, $df = 1, 202$, $P = 0.0072$; Table 2) and accumulated plants more quickly as a function of clump age (ecoregion $\times$ clump age interaction: $F = 7.13$, $df = 1, 202$, $P = 0.0082$).

Mature clumps with multiple plants usually included plants of different ages (i.e., multiple recruitment cohorts). Multiple cohorts were detected in 86% of MD and 91% of CP clumps in the pre-1970 age class. Cohort number per clump also increased with clump age ($F = 197.29$, $df = 1, 204$, $P < 0.0001$), with the rate of increase significantly greater for CP (slope = 0.092) than MD (slope = 0.045) clumps (ecoregion by clump age interaction; $F = 22.19$, $df = 1, 204$, $P < 0.0001$; Fig. 2). This indicates that CP clumps acquired new cohorts at a faster rate than clumps from the MD ecoregion. The ANCOVA including clump age and ecoregion accounted for 51.9% of the variation in cohort number per clump overall. In summary, the number of plants and cohorts per

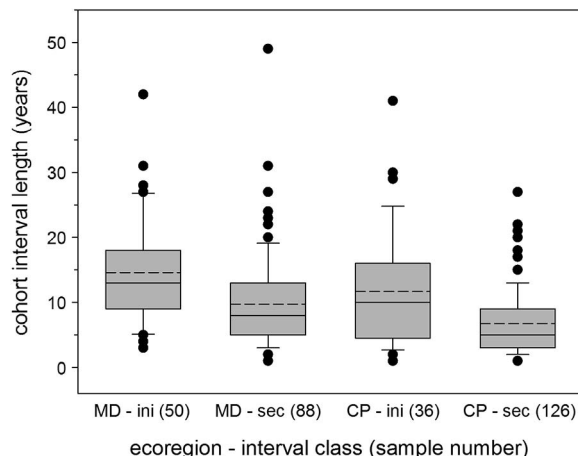


Fig. 3. Cohort interval length (yrs) grouped by ecoregion (Mojave Desert [MD] and Colorado Plateau [CP]) and interval class (initial [ini] and secondary [sec]). Numbers in parentheses indicate sample size for each variable combination. Solid and dashed horizontal lines denote median and mean values, respectively. Differences between ecoregions and interval classes are significant ($P = 0.001$) with no significant interaction.

clump increased with clump age for both ecoregions, whereas the number of plants per cohort remained relatively stable across age classes and regions (Table 2).

Mean cohort intervals were longer for MD clumps (11.5 years) than for CP clumps (7.9 years) across age classes ($F = 10.96$, $df = 1, 296$, $P = 0.0010$; Table 2). The ecoregion-level difference is consistent with the difference in the number of cohorts per clump indicating that, just as CP clumps acquired cohorts at a faster rate than MD clumps, the intervals between CP cohort establishment events were shorter. Secondary interval means (8.0 years) were significantly shorter ($F = 30.14$, $df = 1, 296$, $P < 0.0001$) than initial intervals means (13.4 years) across ecoregions (Fig. 3). We observed a single cohort per clump for a small number (MD = 6; CP = 2) of pre-1970 clumps. Mean estimated clump age for these was 50.6 years, indicating that even though a majority of older clumps possessed two or more cohorts, a few did not add or retain new cohorts over several decades.

Recruitment history

Analysis of recruitment history over the period

1970–2005 demonstrated that blackbrush recruits frequently from seed in both the MD and CP ecoregions (Fig. 4). For our samples, median recruits-per-year was 2.5 for the MD and 4.0 for the CP ecoregions. Recruitment was high (recruits $\geq$ median $\times 4$) for both ecoregions in 1979, 1992, 1998, 2001, and 2003. High to moderate (recruits $\geq$ median $\times 2$) recruitment for one ecoregion coincided with moderate recruitment for the second in 1973, 1975, 1982, 1985, and 1988. Of the 36 years of record, about half (18 MD and 17 CP) produced evidence of very low or null recruitment (0–2 individuals per ecoregion), with 15 of these years shared between ecoregions. Thus, either moderate to high recruitment or null recruitment was synchronized between ecoregions for 25 of the 36 years (69%) of record. High recruitment in MD was paired with low (recruits $<$ median $\times 2$) recruitment for CP in 1990 and 1995 while the opposite was true for 2005. Low levels of recruitment were recorded in both ecoregions for the remaining 8 years of record. Recruitment in years immediately following high recruitment years was low (mean 1.1 plants per year) in comparison to that of all non-high recruitment years combined (mean 2.9 plants per year). Years of high recruitment occurred with approximately equal frequency for MD (7 of 36, 19%) and CP (8 of 36, 22%) while, across all years, observed mean recruitment for CP populations (9.7 per year) was slightly higher than that observed for MD populations (8.3 per year). These patterns emerged even with relatively small sample sizes and in the face of considerable recruitment variability among sites within ecoregions.

Plant growth rate

Across all measured plants, radial growth rate varied from 0.1 to 1.84 mm/year, an 18-fold difference. As expected, mean growth rate differed significantly among competition classes, with 0.68, 0.52 and 0.35 mm/year for low, moderate and high classes, respectively ($F = 130.68$, $df = 2, 631$, $P < 0.0001$; Fig. 5). Within low and high competition classes, mean growth rate did not differ significantly between ecoregions, suggesting similar growth rate potential across the species range; however, within-ecoregion variability was comparatively high, suggesting that the broad categories conceal fine-scale but

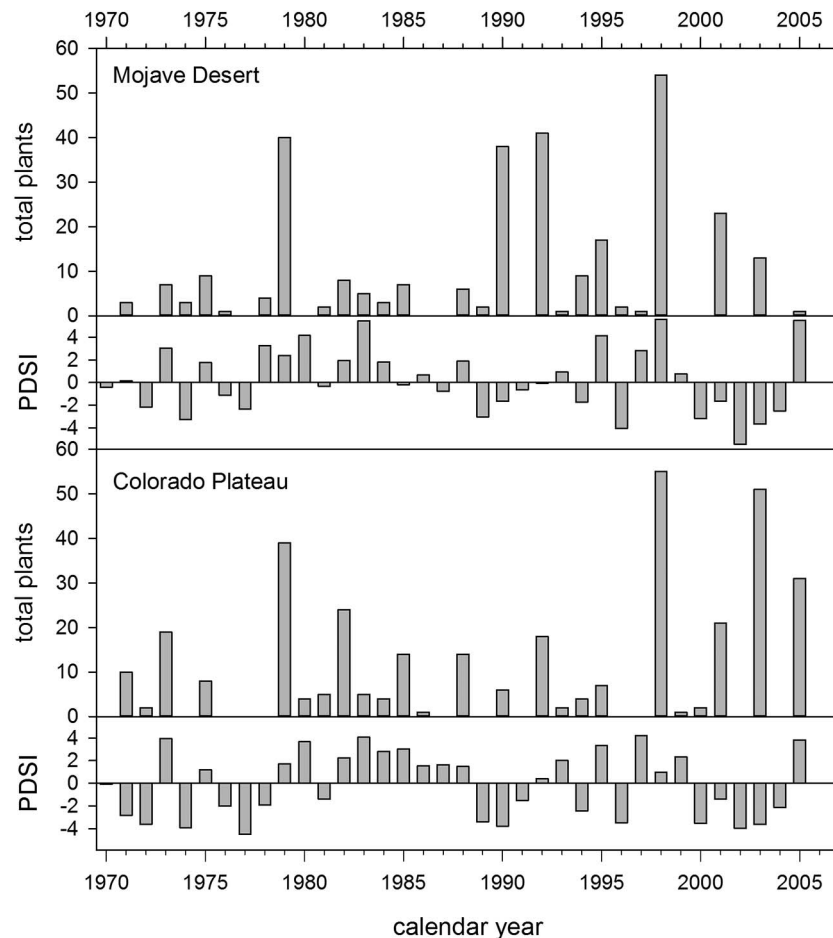


Fig. 4. Recruitment chronologies (1970–2005) indicating germination year for all blackbrush plants with dated piths for Mojave Desert (MD) and Colorado Plateau (CP) ecoregions. Annualized (Oct.–Sep.) Palmer Drought Severity Index (PDSI) values were calculated from PRISM data for Dixie (MD) and Southeast Utah (CP) climate divisions (WWDT 2014). Bars above and below the mid-line indicate wetter and dryer than average conditions, respectively, with bar length an indication of the degree of departure.

meaningful differences in competitive pressure or other factors that act to regulate growth rate. Growth rate for plants in the intermediate competition class differed significantly among ecoregions, with the MD group showing significantly faster growth than the CP group. The reasons for this are not known, but it could be an artifact of small sample size.

We observed major differences in individual growth rate for single-cohort clumps with five or more individuals (moderate competition class). Growth rate of the fastest-growing individual within a group was 1.7–6.5 (mean 3.2) times greater than that of the slowest-growing plant of

the same group (see Fig. 1B). The possible effect of within-group position is unknown, but the notable disparity in growth rate for these same-aged clusters of individuals suggests that, in addition to environmental constraints, relative genotypic fitness among individuals or perhaps emergence priority effects may play a role in dictating variability in within-cohort growth rate.

DISCUSSION

Within-clump plant age distribution

Results from dendrochronological analysis of within-clump age distributions for individual plants demonstrated that adult-size clumps that

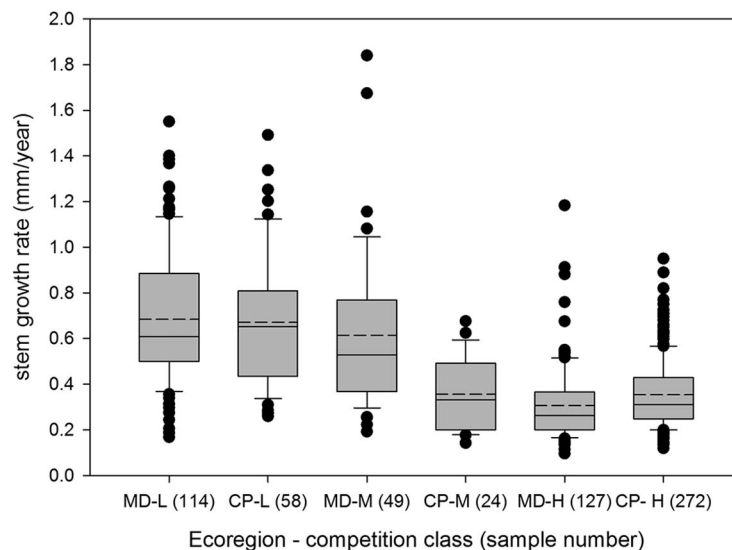


Fig. 5. Stem diameter growth rates (mm/year) for blackbrush plants collected from five Mojave Desert (MD) and four Colorado Plateau (CP) locations. Plants are grouped by ecoregion and presumed levels of intra-specific competition where low (L), moderate (M) and high (H) levels are based upon the presence, number, and relative ages of companion plants (L = plants occurred singly or as members of initial (oldest in clump), low-density (2–4 plants) cohorts; M = plants occurred as members of initial, high-density (5+ plants) cohorts; H = all plants that were members of secondary cohorts (older plants present in the clump)). Numbers in parentheses indicate sample size for each variable combination. Solid and dashed horizontal lines denote median and mean values, respectively.

appear to be single individuals are often comprised of many individuals of multiple ages (study question 1). Genetic analysis of separate stems within a clump indicate that these individuals represent genetically unique entities (B. Richardson, *personal communication*). We also demonstrated unequivocally that blackbrush clumps accrue cohorts as they become older. The rate of accumulation of new individuals differed among ecoregions, with clumps in CP populations acquiring new cohorts at a rate approximately twice that of clumps in MD populations. This difference is surprising, in view of the fact that CP sites generally have less precipitation and colder winters than MD populations. The greater prominence of monsoonal moisture for the CP region vs. the MD region could be a factor in increased juvenile survival. Blackbrush is one of the few shrubs in the CP region that has been demonstrated to use summer moisture, possibly because of its extensive shallow root system (Lin et al. 1996, Summers et al. 2009).

It is important to remember that the age configuration of a blackbrush clump at excavation is a snapshot in time and not a complete clump history. It preserves a record of a minimum number of cohorts and plants that have existed in the clump over time. Documenting past mortality becomes difficult with these methods as dead stem segments deteriorate with time (Milton et al. 1997), but it seems likely that the common pattern is turnover within the clump, with death of individuals of different age classes, but particularly of older plants, and their replacement by younger individuals. The combination of individual plant longevity and periodic within-clump recruitment we detected provides evidence for a self-replacing strategy that appears to account for clump persistence over long periods (study question 1). Repeat photography studies (Webb et al. 1987, 2011) document this kind of clump stability over many decades. We were not able to address questions of potential maximum age limits to individual plants or clumps in this study. We are aware of

one report of an extraordinary plant found on the CP that was estimated to be well over 400 years old (Christensen and Brown 1963); however, locating a plant that has such an extreme age and is sufficiently well preserved for growth-ring-based aging is likely highly unusual, based upon the samples in our study.

The number of plants included in initial cohorts was variable but establishment events were most often represented by single plants. In establishment studies at some of these same sites, ~20–30% of newly emerged seedlings were singles (Meyer and Pendleton 2015b). Heteromyid rodent caches of blackbrush seeds typically include 5–20 seeds (Auger 2005), indicating that partial seed removal often occurs prior to cache emergence. Post-emergence seedling predation and within-cache mortality (thinning) further increases the proportion of single juvenile plants. Although less common in our study, multiple plants often establish and persist as single-cohort clumps for multiple decades, both as initial establishment events and as secondary recruitment into existing clumps.

Recruitment history

For successful recruitment to occur, two conditions must be met, namely, seeds must be present and conditions for establishment must be suitable. Comparisons with reproductive output records over the period 1991–2001 (Meyer and Pendleton 2015a) showed that some years of high recruitment (e.g., 1992, 1998, 2001) followed years of mast seed production (study question 2). The strong recruitment peak in 1979 also likely followed a mast event (S. E. Meyer, *personal observation*). When mast years were followed by drought years, recruitment sometimes failed completely (e.g., 1996). A more common pattern was some level of recruitment even after years of low reproductive output, especially if precipitation was favorable in the follow-up year (e.g., 1995 in the MD ecoregion). The observed low to moderate recruitment following years of low reproductive output could occur in two ways. Low levels of seed production are common in non-mast years. If seed predator populations are low, some of these seeds may either remain undispersed under the maternal plant or may even survive in rodent caches. Alternatively, if the year following mast seed production is

extremely dry, some seeds might remain ungerminated in the seed bank, delaying emergence for more than one year after production. This could account for seedlings that established in 2003 from seeds produced in a mast event in 2001 (Meyer and Pendleton 2015a). There was no seed production and no recruitment in the intervening year (2002), which was the driest year in the period of record. Low recruitment in years immediately following high recruitment years suggests that seed banks were depleted by high recruitment year germination. High establishment in years of moderate drought (1990, 1998, 2001, 2003) indicates that climatic regulation of establishment success is not strong.

Recruitment of new clumps and of new individuals within existing clumps was episodic (Fig. 4) but occurred at surprisingly high frequencies in both ecoregions (Meyer and Pendleton 2015b) revealing complementary strategies for clump initiation and persistence. The high frequency of recruitment is especially notable in view of the fact that all clump samples were obtained from intact stands of blackbrush, where competition from adult plants is expected to be intense (Meyer and Pendleton 2015b). This pattern of regular recruitment from seed into established stands is unusual for a long-lived shrub species in a stressful desert environment (Cody 2000, McAuliffe et al. 2007).

Variability in soil moisture condition was less important in modulating recruitment than expected, with years of successful recruitment spanning a broad range in PDSI (Fig. 4). Conditions or adaptations that enabled blackbrush recruits to establish in dry years (e.g., 1990) are not well understood. Isolated summer storms may have provided drought relief on a local scale. Alternatively, blackbrush seedlings may be capable of escaping drought stress by initiating physiological dormancy at a young age (Ackerman and Bamberg 1974).

Growth rate and the seedling bank

Growth in plant cohort groups containing numerous individuals was somewhat suppressed when compared to that of individual plants and smaller groups (study question 3). It also varied substantially within cohorts, creating seedling size hierarchies (Schwinning and Weiner 1998). The slowest growth rates we observed,

however, were for seedlings established within mature clumps, with stem diameter increase rates as low as 0.1 mm per year. The ability of juvenile blackbrush plants to persist at such low growth rates supports the concept of the 'seedling bank' in this species, i.e., the existence of a pool of suppressed juvenile individuals in closed stands that can potentially respond to gap formation (death of an adult plant in the clump) with increased growth (Grime 1979, Meyer and Pendleton 2015b). The relatively high frequency and the similarity in minimum growth rates observed across dissimilar sites for these suppressed juveniles further supports the idea that the formation of seedling banks is an integral part of blackbrush life history (clump persistence strategy). Because mast seed production and subsequent seedling recruitment are temporally uncoupled from gap formation in closed communities, persistent seed or seedling banks are part of the life history of many masting species, though most reported studies are in forest environments (Tachiki and Iwasa 2010). For species such as blackbrush, that experience intense post-dispersal seed predation, formation of a persistent seed bank is usually under negative selection, emphasizing the importance of a seedling bank for long term stand persistence.

Competition and facilitation effects

Jones et al. (2014) identified a plant interaction gradient among blackbrush sites where nurse plant effects were only positive (facilitation) at a low elevation site (high abiotic stress) but not at a higher elevation site. They also concluded that nurse plants attracted seed predators, decreasing establishment success near established clumps. Conversely, Meyer and Pendleton (2015b) produced evidence that the only facilitative effect of adult blackbrush plants on conspecific seedlings was due to decreased seedling predation (herbivory). In the Meyer and Pendleton study, the positive effect of adult plants on seedling survival at two sites dominated by kangaroo rat seed predators was only observed during the first growing season, when seedlings suffered major predation impacts. In contrast, there was a null or slightly negative effect of adult blackbrush plants on juvenile (post-seedling) survival and growth over the subsequent nine years. The

shorter interval length for recruitment of secondary versus initial cohorts in the present study (Fig. 3) suggests that facilitation increases as clumps mature relative to recently established single-cohort clumps. The potentially lower risk of seed predation for undiscovered seeds that fall among the closely-spaced stems in these well-established clumps would convey an advantage under conditions of high predation.

Evidence for differences in intraspecific competition for seedlings recruiting into clumps versus interspaces in established blackbrush stands as cited in Meyer and Pendleton (2015b) was weak, but there was a very clear increase in both survival and growth rate for blackbrush seedlings establishing on small-scale disturbances (natural gas pipelines) vs. in established stands. This suggests that intraspecific competition in established stands is strong, both under mature plant crowns and in interspaces, and is probably a major factor limiting survival and growth rates of juvenile plants.

Our sampling method provides no estimate of the relative frequency of recruitment into established clumps versus interspaces, but observations made during selection of clumps for sampling indicate that the density of younger clumps is often extremely low, especially at MD sites. At the Legrande site, it was not possible even with extensive searching to locate any small clumps. Population-level clump size class structure data support the conclusion that new clump establishment is generally rare in established stands (S. E. Meyer, *unpublished data*). It seems likely that the seedling bank of suppressed juveniles we detected is concentrated beneath established crowns at most sites.

This study provides evidence of a dual strategy that enables blackbrush to dominate in drought-prone environments. Infrequent new clump recruitment into unoccupied microsites and relatively small-scale disturbances (as observed in Kay 2014) is facilitated by scatterhoarding rodents. Recruitment is possible because mast seed production and variable rodent populations allow a fraction of seeds to escape predation. In a complementary fashion, the ability of seedlings to establish and persist within established clumps provides a ready reserve of replacement plants, the seedling bank, that increases the probability of clump persistence

through time while allowing for individual plant senescence. Together, these strategies allow this slow-growing, non-sprouting species to dominate its habitat in the absence of large-scale disturbance. Both strategies are dependent upon periodic infusion of new propagules. Any disturbance that disrupts the production of those propagules or impedes their dispersal and burial over long periods has the potential to destabilize the system.

Large fires in blackbrush provide a means for testing this disturbance hypothesis. Undisturbed blackbrush communities typically lack a dense herbaceous understory and are therefore relatively resistant to fire. Exotic annual grass invasion, principally of red brome (*Bromus rubens* L.), into MD blackbrush communities has drastically changed the fuels matrix, resulting in several large-scale fires since 2000 (Brooks and Matchett 2006, Brooks et al. 2007). Studies of sites experiencing mid-20th century fires show little to no recovery after several decades (Bowns and West 1976, Callison et al. 1985, Brooks and Matchett 2003, Brooks et al. 2007). This slow recovery is likely due to lack of an in situ seed bank coupled with the inability of heteromyid rodents to quickly disperse seeds the long distances across open ground required to colonize large burned areas (Beatley 1976). The problems of recovery are compounded by exotic annual grass competition. Thus strategies for dominance that have sustained the species for millennia with low levels of disturbance, including regular drought on decadal to centennial scales (Cook et al. 2004, Meko et al. 2007), provide no special adaptation for dominance or even persistence in the face of annual grass weed invasion and the large-scale fires that follow.

ACKNOWLEDGMENTS

We thank S. Clement, S. Decker, B. Richardson, D. Smith, J. Stewart, and T. Stewart for assistance in field work and two anonymous reviewers for suggestions that improved earlier versions of the manuscript.

LITERATURE CITED

- Ackerman, T. L. 1979. Germination and survival of perennial plant species in the Mojave Desert. *Southwestern Naturalist* 24:399–408.
- Ackerman, T. L., and S. A. Bamberg. 1974. Phenological studies in the Mojave Desert at Rock Valley (Nevada Test Site). Pages 215–226 in H. Lieth, editor. *Phenology and seasonality modeling*. Springer-Verlag, New York, New York, USA.
- Ackerman, T. L., E. M. Romney, A. Wallace, and J. E. Kinnear. 1980. Phenology of desert shrubs in southern Nye County, Nevada. *Great Basin Naturalist Memoirs* 4:4–23.
- Auger, J. 2005. Effects of resource availability and food preferences on population dynamics and behavior of Ord's kangaroo rats (*Dipodomys ordii*). Dissertation. University of Nevada, Reno, Nevada, USA.
- Beatley, J. C. 1976. Environments of kangaroo rats (*Dipodomys*) and effects of environmental change on populations in southern Nevada. *Journal of Mammalogy* 57:67–93.
- Bowns, J. E. 1973. An autecological study of blackbrush (*Coleogyne ramosissima* Torr.) in southeastern Utah. Dissertation. Utah State University, Logan, Utah, USA.
- Bowns, J. E., and N. E. West. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southwestern Utah rangelands. Research Report 27. Utah Agricultural Experiment Station, Logan, Utah, USA.
- Brooker, R. R. W., et al. 2008. Facilitation in plant communities; the past, the present and the future. *Journal of Ecology* 96:18–34.
- Brooks, M. L., T. C. Esque, and T. Duck. 2007. Creosotebush, blackbrush, and interior chaparral shrublands. Pages 57–71 in *Fire ecology and management of the major ecosystems of southern Utah*. RMRS-GTR-202. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Brooks, M. L., and J. R. Matchett. 2003. Plant community patterns in unburned and burned blackbrush (*Coleogyne ramosissima*) shrublands in the Mojave Desert. *Western North American Naturalist* 63:283–298.
- Brooks, M. L., and J. R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *Journal of Arid Environments* 67:148–164.
- Callison, J., and J. D. Brotherson. 1985. Habitat relationships of the blackbrush community (*Coleogyne ramosissima*) of southwestern Utah. *Western North American Naturalist* 45:321–326.
- Callison, J., J. D. Brotherson, and J. E. Bowns. 1985. The effects of fire on the blackbrush (*Coleogyne ramosissima*) community of southwestern Utah. *Journal of Range Management* 38:535–538.
- Cawker, K. B. 1980. Evidence of climate control from population age structure of *Artemisia tridentata* Nutt. in southern British Columbia. *Journal of Biogeography* 7:237–248.
- Christensen, E. M., and R. C. Brown. 1963. A blackbrush over 400 years old. *Journal of Range*

- Management 16:118.
- Coates, L. L., K. L. Cole, and J. I. Mead. 2008. 50,000 years of vegetation and climate history on the Colorado Plateau, Utah and Arizona, USA. *Quaternary Research* 70:322–338.
- Cody, M. L. 2000. Slow-motion population dynamics in Mojave Desert perennial plants. *Journal of Vegetation Science* 11:351–358.
- Cole, K. L. 1990a. Reconstruction of the past desert vegetation along the Colorado River using packrat middens. *Palaeogeography, Palaeoclimatology, Palaeoecology* 76:349–366.
- Cole, K. L. 1990b. Late Quaternary vegetation gradients through the Grand Canyon. Pages 240–258 in J. L. Betancourt, T. R. Van Devender, and P. S. Martin, compilers. *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson, Arizona, USA.
- Cook, E. D., C. A. Woodhouse, C. M. Eakin, D. M. Meko, and D. W. Stahle. 2004. Long-term aridity changes in the western United States. *Science* 306:1015–1018.
- Eugenio, M., J. M. Olano, P. Ferrandis, E. Martínez-Duro, and A. Escudero. 2012. Population structure of two dominant gypsophyte shrubs through a secondary plant succession. *Journal of Arid Environments* 76:30–35.
- Génova, M., J. Sánchez-Espejo, F. Dominguez-Lozano, and J. C. Moreno-Saiz. 2013. Dendrochronological study of the endangered shrub *Vella pseudocytisus* subsp. *pau* (Brassicaceae): implications for its recovery and conservation. *Anales del Jardín Botánico de Madrid* 70:178–186.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Grime, J. P. 1979. Primary strategies in plants. *Botanical Journal of Scotland* 43:151–160.
- Holmgren, M., M. Scheffer, and M. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975.
- Hunter, R. 1989. Competition between adult and seedling shrubs of *Ambrosia dumosa* in the Mojave Desert, Nevada. *Western North American Naturalist* 49:79–84.
- Hunter, K. L., and J. R. McAuliffe. 1994. Elevational shifts of *Coleogyne ramosissima* in the Mojave Desert during the Little Ice Age. *Quaternary Research* 42:216–221.
- Jones, L. C., S. Schwinning, and T. C. Esque. 2014. Seedling ecology and restoration of blackbrush (*Coleogyne ramosissima*) in the Mojave Desert, United States. *Restoration Ecology* 22:692–700.
- Kay, C. 2014. Long-term vegetation change in Utah's Henry Mountains: a study in repeat photography. Publication No. BLM-UT-GI-14001-8002. USDI Bureau of Land Management, Utah, USA.
- Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: Why, how, where? *Annual Review of Ecology and Systematics* 33:427–447.
- King, J. E., and T. R. Van Devender. 1977. Pollen analysis of fossil packrat middens from the Sonoran Desert. *Quaternary Research* 8:191–204.
- Lambert, S. E., C. S. Jones, and H. J. Schenk. 2011. Distribution of axis-splitting in Mojave Desert shrub species along an elevational gradient. *Journal of Arid Environments* 75:106–111.
- Lin, G., S. L. Phillips, and J. R. Ehleringer. 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* 106:8–17.
- McAuliffe, J. R. 1986. Herbivore-limited establishment of a Sonoran Desert tree, *Cercidium microphyllum*. *Ecology* 67:276–280.
- McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert plant communities. *American Naturalist* 131:459–490.
- McAuliffe, J. R., E. P. Hamerlynck, and M. C. Eppes. 2007. Landscape dynamics fostering the development of persistence of long-lived creosotebush (*Larrea tridentata*) clones in the Mojave Desert. *Journal of Arid Environments* 69:96–126.
- Meyer, S. E., and B. K. Pendleton. 2005. Factors affecting seed germination and seedling establishment of a long-lived desert shrub (*Coleogyne ramosissima*: Rosaceae). *Plant Ecology* 178:171–187.
- Meyer, S. E., and B. K. Pendleton. 2015a. Evolutionary drivers of mast-seeding in a long-lived desert shrub. *American Journal of Botany* 102:1666–1675.
- Meyer, S. E., and B. K. Pendleton. 2015b. Seedling establishment in a masting desert shrub parallels the pattern for forest trees. *Acta Oecologica* 65–66.
- Meko, D. M., C. A. Woodhouse, C. A. Baisan, T. Knight, J. J. Lukas, M. K. Hughes, and M. W. Salzar. 2007. Medieval drought in the upper Colorado River Basin. *Geophysical Research Letters* 34:L10705.
- Milton, S. J., I. D. Gourelay, and W. R. J. Dean. 1997. Shrub growth and demography in arid Karoo, South Africa: inference from wood rings. *Journal of Arid Environments* 37:487–496.
- Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology* 94:973–979.
- Montgomery, R. A., P. B. Reich, and B. J. Palik. 2010. Untangling positive and negative biotic interactions: views from above and below ground in a forest ecosystem. *Ecology* 91:3641–3655.
- Myers-Smith, I. H., et al. 2015. Methods for measuring arctic and alpine shrub growth: a review. *Earth-Science Reviews* 140:1–13.
- Olano, J. M., M. Eugenio, and A. Escudero. 2011. Site effect is stronger than species identity in driving

- demographic responses of *Helianthemum* (Cistaceae) shrubs in gypsum environments. *American Journal of Botany* 98:1016–1023.
- Pendleton, B. K. 2008. *Coleogyne ramosissima* Torr. Pages 422–425 in F. T. Bonner and R. P. Karrfalt, editors. The woody plant seed manual. Agriculture Handbook 727. USDA Forest Service, Washington, D.C., USA.
- Pendleton, B. K., and S. E. Meyer. 2004. Habitat-correlated variation in blackbrush (*Coleogyne ramosissima*: Rosaceae) seed germination response. *Journal of Arid Environments* 59:229–243.
- Pendleton, B. K., S. E. Meyer, and R. L. Pendleton. 1995. Blackbrush biology: insights after three years of a long-term study. Pages 223–227 in B. A. Roundy, E. D. McArthur, J. S. Haley, and D. K. Mann compilers. Proceedings: wildland shrub and arid land restoration symposium. INT-GTR-315. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Poore, R. E., C. A. Lamanna, J. J. Ebersole, and B. J. Enquist. 2009. Controls on radial growth of mountain big sagebrush and implications for climate change. *Western North American Naturalist* 69:556–562.
- Richardson, B. A., S. G. Kitchen, R. L. Pendleton, B. K. Pendleton, M. J. Germino, G. E. Rehfeldt, and S. E. Meyer. 2014. Adaptive responses reveal contemporary and future ecotypes in a desert shrub. *Ecological Applications* 24:413–427.
- Richardson, B. A. and S. E. Meyer. 2012. Paleoclimate effects and geographic barriers shape regional population genetic structure of blackbrush (*Coleogyne ramosissima*: Rosaceae). *Botany* 90:293–299.
- Roughton, R. D. 1972. Shrub age structures on a mule deer winter range in Colorado. *Ecology* 53:615–625.
- Schweingruber, F. H., and P. Poschod. 2005. Growth rings in herbs and shrubs: life span, age determination and stem anatomy. *Forest Snow and Landscape Research* 79:195–415.
- Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113:447–455.
- Seligman, N. G., and H. Zalmen. 2000. Regeneration of a dominant Mediterranean dwarf-shrub after fire. *Journal of Vegetation Science* 11:893–902.
- Silvertown, J., and D. Charlesworth. 2001. Introduction to plant population biology. Fourth edition. Blackwell Science, London, UK.
- Smith, S. D., E. Naumburg, U. Niinemets, and M. J. Germino. 2004. Leaf to landscape. Pages 262–294 in W. K. Smith, T. C. Vogelmann, and C. Critchley, editors. Photosynthetic adaptation. Springer, New York, New York, USA.
- Srur, A. M., and R. Villalba. 2009. Annual growth rings of the shrub *Anarthrophyllum rigidum* across Patagonia: interannual variations and relationships to climate. *Journal of Arid Environments* 73:1074–1083.
- Stokes, M. A. and T. L. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois, USA.
- Summers, H. A., B. N. Smith, and L. D. Hansen. 2009. Comparison of respiratory and growth characteristics of two co-occurring shrubs from a cold desert, *Coleogyne ramosissima* (blackbrush) and *Atriplex confertifolia* (shadscale). *Journal of Arid Environments* 73:1–6.
- Tachiki, Y., and Y. Iwasa. 2010. Both seedling banks and specialist seed predators promote the evolution of synchronized and intermittent reproduction (masting) in trees. *Journal of Ecology* 98:1398–1408.
- Valladares, F., J. Zaragosa-Castells, D. Sanchez-Gomez, S. Matesanz, B. Alonso, A. Portsmouth, A. Delgado, and O. K. Atkin. 2008. Is shade beneficial for Mediterranean shrubs experiencing periods of extreme drought and late-winter frosts? *Annals of Botany* 102:923–933.
- Van Devender, T. R. 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. Pages 134–165 in J. L. Betancourt, T. R. Van Devender, and P. S. Martin, compilers. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson, Arizona, USA.
- Webb, R. H., J. Belnap, M. L. Scott, and T. C. Esque. 2011. Long-term change in perennial vegetation along the Colorado River in the Grand Canyon National Park (1889–2010). *Park Science* 28:73–77.
- Webb, R. H., J. W. Steiger, and R. M. Turner. 1987. Dynamics of Mojave Desert shrub vegetation in the Panamint Mountains. *Ecology* 50:478–490.
- West, N. E. 1983. Colorado Plateau-Mohavian blackbrush semi-desert. Pages 399–411 in N. E. West, editor. Temperate deserts and semi-deserts. Elsevier, Amsterdam, The Netherlands.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities: numerical relations of species express the importance of competition in community function and evolution. *Science* 147:250–260.
- Wright, A., S. A. Schnitzer, and P. B. Reich. 2014. Living close to your neighbors: the importance of both competition and facilitation in plant communities. *Ecology* 95:2213–2223.
- WWDt [WestWide Drought Tracker]. 2014. Desert Research Institute (DRI), University of Idaho. <http://www.wrcc.dri.edu/wwdt/>