

Blackbrush Biology: Insights After Three Years of a Long-Term Study

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Abstract—Blackbrush (*Coleogyne ramosissima*, Rosaceae) is one of the least studied of the landscape-dominant shrubs in the western United States. Previous studies have been limited to relatively small geographic areas. No studies have examined the variability of blackbrush across its range. We have begun a series of long-term studies of blackbrush biology, establishing study sites across a large portion of the shrub's range. Studies deal with: (1) reproductive biology, including factors influencing flowering and fruit set, (2) seed germination biology (laboratory and field studies), (3) seedling emergence, survival, and growth rate, (4) population size and structure, and (5) community relationships. We present data from the 1991 to 1993 growing seasons. While some of these data are preliminary, results indicate the need to reevaluate the classification of blackbrush as a paleoendemic species (ancient taxa with restricted distribution) that possesses little genetic variation. Data from these studies also provide insights into the problems of blackbrush community restoration.

Before beginning our studies on blackbrush (*Coleogyne ramosissima*, Rosaceae), we reviewed the available literature to learn what was known about the species and to identify areas of research that might prove fruitful. It quickly became apparent that there are many conspicuous gaps in the knowledge of blackbrush biology. In most definitive study of blackbrush to date, Bowns (1973) listed areas needing additional research. Many of these areas remain to be addressed. Most studies were conducted at either the Nevada Test Site (Clark County, NV) or in southwestern Utah (primarily western Washington County). No one has studied blackbrush across the whole of its range or made comparisons outside of a local area. Yet, while no such comparisons have been made, Stebbins and Major (1965) are often cited by authors categorizing blackbrush as a species of low variability. We are attempting to address the lack of data on blackbrush variability with our studies.

In defining our research goals, we took into account not only the gaps in existing knowledge, but also techniques

commonly used in our laboratory when studying other species. Reproductive biology, including pollination, fruit production, seed germination, and seedling establishment, is critical to understanding the population dynamics of blackbrush. Therefore, it is the prime focus for our initial studies. The series of studies was designed to provide broad, integrated knowledge of the biology of blackbrush. We expect that this knowledge will be useful in designing protocols for the successful management and revegetation of blackbrush communities.

Research in Progress

We began our series of studies on blackbrush biology in 1991. After viewing as much of the range of blackbrush as possible, we selected representative study sites that included a variety of soil types, elevations, and as broad a geographic range as we could cover. Seeds were collected from 30 locations (from southeastern Nevada to eastern Utah) for laboratory and field germination studies. Fifteen long-term sites were established to look at flowering intensity, reproductive output, and community structure. In 1992, we tagged approximately 2,000 natural seedling caches at four locations; two in the Mojave Desert and two on the Colorado Plateau. These seedlings emerged from heteromyid rodent (primarily pocket mice and kangaroo rats) scatter hoards, seeds the rodents place in shallow depressions and cover with soil (Longland 1994). At three of the four locations, additional transects were established on adjacent pipeline corridors to examine natural recruitment on small-scale disturbances. We also followed seedling emergence and survival from artificial scatter hoards at two locations. The pollination biology of blackbrush was studied at three locations over a 2-year period beginning in 1992. A brief synopsis of these studies is given below. The complete results have been or will be published in more detail elsewhere.

Reproductive Biology

Flowering in blackbrush is induced by moderate to heavy winter precipitation (Beatley 1974). Flowering on individual plants is not synchronous, occurring over a period of 1 to 2 weeks. Flowering in the population lasts from 2 to 3 weeks (Bowns and West 1976, personal observation). Prior to our work, the pollination system had been postulated as either wind pollinated (McArthur 1989) or insect pollinated (Pendleton and others 1989).

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Our studies have demonstrated that blackbrush is wind pollinated (Pendleton and Pendleton 1994). Net bags that excluded insect pollinators had no significant effect on fruit set when compared with open-pollinated branches. Results were consistent among the three study sites.

Blackbrush is also highly self-incompatible (the plants do not self pollinate). The overall fruit set for selfed branches was 3.4 percent, compared with 39.9 percent for open-pollinated branches. Production of fruit within bakery bags to which outcross pollen had been added (29.2 percent fruit set) demonstrates that the lack of fruit production within the selfed bags was not due to conditions within the bag. Self-incompatibility is known in other shrubby genera of the Rosoideae (Blauer and others 1975; McArthur 1989; Pendleton and McArthur 1994).

Blackbrush exhibits several characteristics that would indicate a switch from insect to wind pollination in the recent geologic past. The large, bright yellow-green calyx would appear to be attractive to pollinators. However, we did not observe any pollinator activity during our field work. The occasional presence of yellow petals (Welsh and others 1987) lends additional support to this hypothesis.

Significant differences in fruit set also occur among populations and among individual plants (Pendleton and Pendleton 1994). The adjusted fruit set (fruit set divided by percent fill) for 15 open-pollinated populations ranged from 3 to 72 percent (Meyer and Pendleton, unpublished data). Differences in fruit set among individual plants and populations likely reflect differences in resource reserves and the degree of resource replenishment since the last major fruiting event. Even when winter precipitation is adequate for flower initiation occurs in successive years, blackbrush does not produce successive large fruit crops (Meyer and Pendleton, unpublished data). This suggests that blackbrush is a mast fruiting species, and that the size of the fruit crop is a function of available stored resources. Studies in progress are intended to clarify the respective roles of weather and resource reserves in mast fruiting cycles.

Seed Germination

Seed germination in our field studies occurred from December to February, with seedling emergence approximately 1 month later (Pendleton and Meyer 1994b). During the period between radicle emergence and cotyledon emergence, stored resources produce several inches of root growth. Bowns and West (1976) also report March emergence for populations in southwestern Utah. Seedling emergence has been reported as early as November (Graham 1994).

Blackbrush seed, when freshly collected, is largely dormant (the mean from our collections was approximately 65 percent dormant). Laboratory-stored seed maintained dormancy through the first 4 months of storage. In contrast, seeds cached in retrieval bags during the same 4 months (ending in November) were only 10 percent dormant at the Hurricane field site and only 50 percent dormant at the Arches field site. After 6 months, field-stored seed was 100 percent nondormant at both sites, and the seed never reentered dormancy. Laboratory-stored seed was only 50

percent nondormant after 10 months of storage. Our working hypothesis is that summer and fall rains reduce initial dormancy under field conditions; winter chilling removes any remaining dormancy (Pendleton and Meyer 1994a,b, unpublished data).

A significant relationship exists between collection-site elevation and seed germination response at 5 to 15 °C, with and without a short (2-week) chill (Pendleton and Meyer 1994a). Seeds collected from low-elevation sites were less dormant than seeds from high-elevation sites. Seeds from all elevations responded positively to a 2-week chill, but the response of seeds from low-elevation sites was roughly twice that of seeds collected at high-elevation sites. Data from our low-elevation (Clark County, NV, and Washington County, UT) sites are comparable to the germination characteristics and chill responses reported for similar locations by Wallace and Romney (1972) and by Bowns and West (1976). These authors did not, however, examine seeds collected from high-elevation sites, which yield quite different results.

Seed from a site near Hurricane, Washington County in southwestern Utah, and from Arches National Park, in southeastern Utah, were used in reciprocal seedling emergence trials. Multiple lots of seeds from both Hurricane and Arches were cached at both sites. Percent emergence and survivorship was highest for Arches seed at the Arches site, and for Hurricane seed at the Hurricane site (unpublished data). These data and the previously discussed correlation between dormancy status and elevation of the collection site strongly suggest that—at least for germination and establishment ecology—blackbrush has evolved ecotypes.

Establishment Ecology

Blackbrush is cached in scatter hoards by heteromyid rodents. The fate of scatter hoard seed was addressed by examining seedling survival in natural caches, as well as emergence and survival of artificial caches. Cache survival, the percentage of natural caches with at least one surviving seedling, varied from 1.4 to 90.2 percent for the period from emergence through two growing seasons (Meyer and Pendleton unpublished data). Percent seedling survival and percent cache survival were lowest on Mojave Desert sites and highest on Colorado Plateau sites. Personal observations during our field travels and community size-class data corroborate this finding; seedling survivorship and frequency of recruitment episodes are higher on the Colorado Plateau than in the Mojave Desert.

Seedling and cache survival are influenced by a number of factors. Most mortality of natural scatter hoards took place early in the first year. Early spring mortality was primarily due to animals grazing the new sprouts. Mortality due to drought occurred in late May through early June (Meyer and Pendleton, unpublished data). A majority of seedlings and caches that survived the first summer also survived through the second summer.

During our field trips, we observed recruitment on small-scale disturbances. We paired transects of natural seedling caches on pipeline rights-of-way with similar transects in established stands. Survivorship on the pipeline rights-of-way was higher, particularly for transects in the Mojave

Desert. This may indicate that mature stands tie up resources and space, excluding seedling establishment. When space becomes available, seedlings can become established.

Reestablishing blackbrush following disturbance is an increasingly important issue. Mining and fire disturb the most acreage in the blackbrush community. There are two reports of blackbrush reestablishing after fire (Bates 1984; Thatcher 1975), but these reports are the exception. As a rule, blackbrush does not reestablish after fire (Bowns and West 1976; Callison and others 1985). Possible hypotheses for the lack of natural reestablishment following burning are:

(1) Lack of seed. Blackbrush does not form long-term seedbanks, and mast events that produce short-term seedbanks are relatively rare (Meyer and Pendleton, unpublished data). If no scatter hoards are established in the year or two before a burn, reestablishment would depend upon rodents transporting seed from unburned areas out onto the burn, an unlikely possibility for large disturbances. We suggest that the reports by Thatcher (1975) and Bates (1984), in which blackbrush reestablished following fire, represent cases in which a short-term seedbank was in place.

Habitat preference by scatter hoarding rodents may also be a factor. Beatley (1976) reported that, on the Mojave, the kangaroo rat, *Dipodomys microps*, occupies blackbrush communities to the exclusion of other species of kangaroo rat. In contrast, *D. merriami* occupies open and disturbed habitats. In the event of fire in blackbrush, *D. microps* is displaced by *D. merriami* on the burn. Seed transport from the blackbrush community onto the burn would be minimal, at least in the Mojave Desert.

(2) Blackbrush is slow-growing, and is not competitive with pioneering species after a burn.

(3) Fire or the introduction of exotic annuals alters the soil microflora to the detriment of blackbrush establishment. These and other hypotheses should be tested.

The establishment of a cohort of blackbrush seedlings is the result of a set of events, some independent and some interrelated. Based on the literature and on our experiments and observations, the following sequence of events is necessary for blackbrush seedlings to become established.

(1) Precipitation in the fall and winter must be sufficient to trigger massflowering (Beatley 1974).

(2) The plant must have sufficient resource reserves to support flowering and fruit production. Blackbrush is a mast flowering and fruiting species; it doesn't produce large fruit crops in successive years even if rainfall is adequate (Meyer and Pendleton, unpublished data). Ongoing experiments will show the time between mast events under a variety of rainfall regimes.

(3) Blackbrush seeds are cached in scatter hoards by heteromyid rodents. For seedling establishment, there must be enough rodents to process the seed and enough seed so the rodents do not consume all or most of the scatter hoards (Longland 1994). Rodents excavate and consume seeds from the time the seeds are first buried until well after the seedlings have emerged (personal observations). If only a small number of seedlings survive this "rodent sieve," drought-related mortality generally eliminates the

remaining seedlings. Mast fruit crops provide sufficient seed so the potential exists for a cohort to establish.

(4) Rainfall must be adequate to trigger germination (Beatley 1974).

(5) Rainfall must be adequate during the spring and early summer to support the establishment of seedlings. Moisture for seedling establishment may be an important limiting factor in the drier *Coleogyne-Larrea* ecotone, where moisture is sufficient to support adult blackbrush plants but may be insufficient to establish seedlings (Beatley 1975). In our studies, the vast majority of seedling mortality occurred between emergence and midsummer, when seedling growth ceases and dormancy occurs (Meyer and Pendleton, unpublished data).

(6) Space and resources must be sufficient to support new plants. Undisturbed mature blackbrush stands may be "closed" (with their resources locked up); young plants are often very rare. When openings occur in mature stands due to small-scale disturbances, seedling recruitment is evident in many cases (personal observations).

We hope this model will be useful as we work to develop techniques for revegetating blackbrush from seed.

Conclusions

Classification of blackbrush as a paleoendemic (Stebbins and Major 1965) is appropriate in that *Coleogyne* is a monotypic genus, has no close relatives, and its relationship to other taxa within the Rosaceae is unclear (Morgan and others 1994). However, this classification is not particularly relevant to the management of blackbrush communities. What is relevant is that *Coleogyne* is an ecotonal species. Ecotonal species under changing climatic conditions are subjected to a suite of selection pressures. Three natural outcomes of these selection regimes are: (1) the species becomes extinct, unless (2) the species possesses a wide range of tolerance or evolves new ranges of tolerance in response to the change in climate, or (3) the species migrates with the ecotonal boundary. While ecotonal species are tracking the climatic conditions to which they are best adapted, they may also have to adapt to new edaphic (soil) conditions (Stebbins and Major 1965).

We have demonstrated ecotypic variation in characters that are important to the establishment of blackbrush seedling cohorts. We have also demonstrated high rates of seedling establishment and relatively frequent seedling establishment events in blackbrush communities of the Colorado Plateau. We hypothesize that blackbrush is a fairly recent arrival to at least some areas on the Colorado Plateau, and that it is migrating into areas where it is adapted to the edaphic and climatic conditions.

Examination of the paleoecological literature reveals two important points relevant to blackbrush ecotones. First, during the Quaternary (the most recent geologic period), the *Coleogyne-Larrea* ecotone has undergone frequent migrations in response to climatic shifts. Secondly, evidence from packrat middens demonstrates that blackbrush has repeatedly moved up and down elevational gradients in response to shifts in temperature and rainfall patterns (Cole and Webb 1985; Phillips and Van Devender 1974;

Tausch and others 1993; Spaulding 1990). In contrast, Wells (1983) states that, on the high deserts of the Mojave, blackbrush has persisted more or less in place, while woodland conifer species with which it formerly was associated are now found at much higher elevations.

The paleoecological evidence and the results of our research argue against labeling blackbrush as a paleoendemic species with little variation and, perhaps, on the way to extinction. A species with ecotypic variation, the gene pool necessary to evolve new ranges of tolerance in place, and that has migrated successfully along environmental gradients certainly does not fit this label.

Management of ecotonal species is a challenge, and blackbrush is no exception. Continued research is needed to acquire knowledge for successful management of blackbrush in the face of more frequent large fires, disturbances such as roadbuilding and mining that require revegetation, and changes in community composition caused by the invasion of exotic species.

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