



## Original article

## Seedling establishment in a masting desert shrub parallels the pattern for forest trees

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## ABSTRACT

The masting phenomenon along with its accompanying suite of seedling adaptive traits has been well studied in forest trees but has rarely been examined in desert shrubs. Blackbrush (*Coleogyne ramosissima*) is a regionally dominant North American desert shrub whose seeds are produced in mast events and scatter-hoarded by rodents. We followed the fate of seedlings in intact stands vs. small-scale disturbances at four contrasting sites for nine growing seasons following emergence after a mast year. The primary cause of first-year mortality was post-emergence cache excavation and seedling predation, with contrasting impacts at sites with different heteromyid rodent seed predators. Long-term establishment patterns were strongly affected by rodent activity in the weeks following emergence. Survivorship curves generally showed decreased mortality risk with age but differed among sites even after the first year. There were no detectable effects of inter-annual precipitation variability or site climatic differences on survival. Intraspecific competition from conspecific adults had strong impacts on survival and growth, both of which were higher on small-scale disturbances, but similar in openings and under shrub crowns in intact stands. This suggests that adult plants preempted soil resources in the interspaces. Aside from effects on seedling predation, there was little evidence for facilitation or interference beneath adult plant crowns. Plants in intact stands were still small and clearly juvenile after nine years, showing that blackbrush forms cohorts of suppressed plants similar to the seedling banks of closed forests. Seedling banks function in the absence of a persistent seed bank in replacement after adult plant death (gap formation), which is temporally uncoupled from masting and associated recruitment events. This study demonstrates that the seedling establishment syndrome associated with masting has evolved in desert shrublands as well as in forests.

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## 1. Introduction

Masting, defined as the synchronous intermittent production of large seed crops by perennial plants, is a well-known phenomenon that has been investigated empirically for a wide range of species (Kelly and Sork, 2002) and that has recently received considerable theoretical attention (Tachiki and Iwasa, 2010, 2012; Kelly et al., 2013; Tamburino and Bravo, 2013). A frequently proposed explanation for the evolution of masting is predator satiation (Janzen, 1971; Silvertown, 1980; Kelly, 1994). The production of a large seed crop following inter-mast years with low seed production is thought to permit escape of some fraction of the mast year crop from seed predators, whose numbers have declined during the

inter-mast years and do not respond quickly enough to take full advantage of the resource pulse represented by masting. The seed predators may be pre-dispersal predators that consume seeds, or they may be post-dispersal predators that often carry out secondary dispersal of seeds as well as consuming them. One of the best studied systems is scatter-hoarding, in which the vertebrate predator, usually a rodent or bird, removes seeds from the vicinity of the parent plant and caches them in shallow surface scatter-hoards or caches that may provide an optimum environment for seedling establishment (VanderWall, 2010). In inter-mast years when seed resources are limiting, few or no seeds remain in scatter-hoards to emerge in spring. It is only immediately following mast years that some seeds remain in caches long enough to produce emerged seedlings.

High post-dispersal seed predation may select for seeds that do not form persistent seed banks, yet mast events are rarely tied

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temporally to the disturbance regimes that create openings for new plants in closed communities. For these reasons a common pattern in masting tree species is the formation of 'seedling banks' (Grime, 1979). These plants establish after mast events, grow very slowly, and remain in the juvenile condition for extended time periods, largely because their growth is suppressed by competition from conspecific adults. These suppressed plants are poised to resume normal growth when gap formation takes place (Szwagrzyk et al., 2001; Alvarez-Aquino and Williams-Linera, 2002; Cruz-Rodriguez and Lopez-Mata, 2004; Antos et al., 2005). They are often the primary source of new trees following the loss of adult trees in forests, for example, following insect outbreaks (DeRose and Long, 2010; Rossi and Morin, 2011).

Conspicuously lacking in the large body of knowledge on masting is any explicit discussion of mast seeding in deserts. The high inter-annual variability in seed production observed in deserts is usually assumed to be a direct consequence of differences in current-year growing season quality due to variation in the amount and timing of precipitation (Beatley, 1974). By scaling seed production to current-year growing conditions, desert perennials may maximize seed production over time (resource matching; Kelly and Sork, 2002). This reproductive schedule does little to protect seeds from predation, however, because seed predators are presumably tracking the same variation in resource quality as plants.

Seed predators are prominent members of the fauna of desert systems (Brown et al., 1979a). Post-dispersal predation by rodents and ants has been particularly well-studied, though the primary focus of these studies has been seed resource variation due to inter-annual variation in seed production by annual plants (Beatley, 1976; Brown et al., 1979b; Inouye et al., 1980). Annual plant seed production is strongly constrained by current-year growing conditions (Beatley, 1974). In contrast, perennial plants, particularly shrubs, have the potential to produce large seed crops in non-optimal years, if such production increases the fitness of the maternal plant by improving chances of offspring survival. This suggests that mast seeding in desert shrubs could be under positive selection.

The Rosaceous desert shrub *Coleogyne ramosissima* Torr. (blackbrush), a regionally important species along the ecotone between North American warm and cold deserts, exhibits a masting pattern of inter-annual seed production (Pendleton et al., 1995; Pendleton and Meyer, 2004; Auger, 2005). This wind-pollinated species (Pendleton and Pendleton, 1998) forms nearly monospecific stands over large areas on the shallow, infertile soils where it is the dominant shrub (West, 1983). We took advantage of a mast year (1991) to initiate a series of short and long term studies on the regeneration biology of this little-studied shrub (Pendleton et al., 1995; Pendleton and Pendleton, 1998; Pendleton and Meyer, 2004; Meyer and Pendleton, 2005). These included experimental studies on seed germination and seedling establishment at

climatically contrasting sites in the Mojave Desert (near Hurricane, UT), and on the Colorado Plateau (Salt Valley in Arches National Park, UT; Meyer and Pendleton, 2005). In the spring of 1992, the year following the masting event, we observed emergence of thousands of blackbrush seedlings in clusters from apparent rodent caches at numerous sites across the species range. We followed the fate of the seedlings in these natural caches from emergence through nine growing seasons at four sites chosen to represent a range of climate and soil conditions.

Here we use this nine-year data set to address the hypothesis that establishment patterns exhibited by blackbrush following a mast event are associated with a suite of seed and seedling traits similar to those exhibited by masting species of mesic environments (Tachiki and Iwasa, 2010). We also examine how establishment patterns are mediated through the actions of rodent seed predators that are also agents of dispersal for this species. Specifically, we tested the hypothesis that recruitment, establishment, and growth patterns in blackbrush would result in the formation of 'seedling banks', a key component of the masting syndrome in forest species.

## 2. Materials and methods

We tagged naturally emerging seedlings in spring 1992 at two sites where we had established experimental seeding studies the previous year (Meyer and Pendleton, 2005). These were sandy sites with relatively deep soils, but with contrasting climates (Hurricane and Salt Valley; Table 1). We also tagged naturally emerging seedlings at two additional sites with climates somewhat similar to the original sites, but with shallower, rocky soils (Toquerville and Little Rockies).

Newly emerged blackbrush seedlings were enumerated at each of the four study sites in early to mid-March 1992 by establishing belt transects and tagging and noting the coordinates of all caches observed within each transect. We used numbered aluminum tags on nails flush with the surface to mark the caches, placed approximately 15 cm from the cache in a standard relative position to reduce the possibility of behavioral effects. The transects had a standard width of 5 m but varied in length and total area depending on cache density, so that approximately 400 caches were tagged in intact stands at each site (Table 2). At three of the sites, we also established transects on small-scale disturbances (natural gas pipeline corridors at Salt Valley and Toquerville and an abandoned powerline road at Hurricane). Cache densities were lower on disturbances, resulting in lower numbers of tagged caches (ca. 140–190; Table 2).

At the time of tagging, we counted the number of seedlings in each cache and noted any apparent rodent activity (e.g., excavation). We also noted the position of the cache relative to established

**Table 1**

Location and site information for four research sites included in the study. Climate data are from: [www.prism.oregonstate.edu/](http://www.prism.oregonstate.edu/).

	Salt Valley	Little Rockies	Hurricane	Toquerville
Latitude	38° 45' 40.65" N	37° 45' 35.54" N	37° 10' 33.30" N	37° 16' 47.82" N
Longitude	109° 36' 02.04" W	110° 39' 06.30" W	113° 20' 18.50" W	113° 18' 41.20" W
Elevation (m)	1497	1700	985	1164
Substrate	Aeolian sand over sandstone	Gravelly alluvium quartz monzonite	Aeolian sand and gravel over basalt	Gravelly alluvium over basalt
Soil Depth (cm)	77	24	74	44
% Surface Rock	<5	60	20	50
% Cryptogamic Crust	30	<10	<5	<5
Slope	10–20%	10–15%	10–15%	5–10%
Aspect	SSW	N	S	SE
Mean Annual Temperature (C)	12.1	12.2	16.7	15.6
Annual Precipitation (mm)	242	230	280	321

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