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Mortality over 16 years of cacti in a burnt desert grassland

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Abstract

Mortality of cacti after grassland fires is usually <25% within 2 years. Little, however, is known about long-term mortality. This study followed the fate of 50 marked plants of each of four species of small cacti (*Coryphantha vivipara*, *Echinocereus pectinatus*, *Echinomastus intertextus* and *Mammillaria heyderi*) on burnt and unburnt desert-grassland in Arizona. All marked plants were dead within 16 years. The first three species suffered increased mortality after being burnt while *M. gummifera* survived better after fire. The average rate of mortality of burnt plants over unburnt plants was 10.2 times higher in *E. pectinatus*, 3.7 times in *C. vivipara* and 1.5 times in *E. intertextus*. In *M. heyderi*, however, the mortality of burnt plants was 0.25 that of control plants. Fire more rapidly removed the breeding populations of the first three species, reducing seed availability in the occasional years favourable for establishment, increasing the risk of local extinction. Cacti did establish on the study areas and by the end were of a similar size to the dead cohort giving the superficial impression that the site was unchanged except for a reduction on unburnt sites in total cactus density (burnt: 445/ha in 1987, 401/ha in 2003; control: 2235/ha and 675/ha, respectively). Evidence of fire and dead plants rapidly disappeared, so without plants being marked the death of one population and establishment of another would have been easily missed. Estimates of growth rates support the assertion that the final plants established during the study.

Introduction

Many cacti in N. America are found in shrublands and grasslands that are prone to naturally occurring fires (e.g. Wright and Bailey 1982). Moreover, the majority of species tend to live embedded within the vegetation, rather than on rocky areas devoid of fuel (Thomas 1991), and so are likely to be burnt during a fire. Previous studies have shown that short-term mortality of cacti after fire is variable, often more than 50% but rarely total (Reynolds and Bohning 1956; Cable 1967; O'Leary and Minnich 1981; Cave and Patten 1984; Zschaechner 1985; Brown and Minnich 1986). If mortality on unburnt control areas is assumed to represent background non-fire mortality on burnt sites, death attributable to fire is usually <25% (Humphrey and Everson 1951; Thomas and Goodson 1992).

The above studies followed mortality for up to 2 years after the fire, but there is some evidence that mortally wounded cacti may continue to die over a longer period resulting in drastic underestimation of fire-induced mortality. Post-fire death of larger cacti such as *Opuntia* spp., *Ferocactus* spp. and *Carnegiea gigantea* may be clearly visible within a year (Heirman and Wright 1973; McLaughlin and Bowers 1982) but further mortality may be evident after 2–3 years (Bunting et al. 1980; Wright and Bailey 1982) and even after 4–6 years (Cable 1967, Rogers 1985). Fewer long-term studies have been conducted on smaller and less conspicuous species that are generally < 25 cm tall, but these suggest that they are also prone to delayed mortality. A study by Bunting et al. (1980) in the mixed prairie of Texas showed that the mortality of the small-growing *Coryphantha vivipara* was complete within one year but *Echinocactus texensis*, *Mammillaria heyderi* and *Echinocereus reichenbachii* mortality increased from < 35% after one year to > 70% after 3 years. Unfortunately there were no unburnt control plants in this study so it is difficult to judge how many of these plants would have died anyway. If fire is responsible for a higher rate of long-term mortality than on unburned areas, there are important implications for the use of fire as a management tool to control shrub invasion (e.g. Drewa and Havstad 2001). This study follows the fate of individuals of four species of small-growing cactus on burnt and unburnt desert-grassland in Arizona over 16 years.

Methods

The study was carried out at the Appleton–Whittell Research Ranch, Elgin, Southern Arizona (31°39′ N, 110°32′ W), some 100 km Southwest of Tucson, in an area of semi-desert grassland (*sensu* Brown 1982) on rolling topography. The 3160 ha ranch is a sanctuary of the National Audubon Society, minimally managed as a biodiversity preserve and natural ecological laboratory, and has been ungrazed by livestock since 1967 (Bahre 1977) with only limited subsequent grazing primarily by pronghorn (*Antilocapra americana* Ord) and several species of deer. The resulting, largely undisturbed vegetation is dominated by the grasses *Bouteloua* spp. (HBK) Lag. ex Griff. with *Eragrostis intermedia* Hitch. and *Lycurus phleoides* HBK (Bock and Bock 1992). Four species of small cactus are common in this vegetation: *Coryphantha vivipara* (Nutt.) Brit. & Rose, *Echinocereus pectinatus* (Scheidw.) Engelm., *Echinomastus intertextus* (Engelm.) Brit. & Rose (= *Neolloydia intertexta* (Engelm.) L. Benson) and *Mammillaria heyderi* Muenl. (= *M. gummifera* Engelm.); names follow Flora of North America Editorial Committee (1993). The first three are globular/columnar cacti normally < 30 cm tall while *M. heyderi* grows from a large subterranean tap-root with the plate-like top of the plant usually no more than 2–4 cm above the soil surface.

Field sites

Following several hot dry months (< 3 cm of rain in 10 weeks), wildfire burned over a thousand hectares of the grassland on 16–17 July 1987. The herbaceous vegetation was almost uniformly burnt-off leaving the cacti scorched over normally the entire epidermis except for a ring of green tissue < 1 cm high around the base of the plant. Fire frequency is difficult to estimate but six major fires have burnt portions of the ranch in the last 30 years (Bahre 1977, Bock and Bock 2000). It is estimated that fire had not burnt the areas used in this study since at least 1975.

Due to practical constraints the study was initially restricted to one burnt area (0.8 ha) and one nearby unburnt control area (0.6 ha). Very few *Echinocereus pectinatus* could be found on the burnt site, so for this species a second nearby area (0.5 ha) that had burnt in May 1987 (i.e. two months earlier) was used. The three areas were within 1.5 km of each other and were similar in altitude (c. 1500 m), slope (< 10°), aspect and soil structure (estimated from soil pits). It was judged from ranch records and aerial photographs that the three sites were similar in vegetation composition prior to burning, and carried the same plant biomass (0.5–1.0 kg/m^2) – estimated from nearby unburnt vegetation for the burnt areas. The single big difference between the three areas was the initial densities of cacti (Figure 1) attributed to very local variations in rainfall and seedling establishment conditions in previous years.

It is acknowledged that the use of unreplicated areas is a design weakness but it is considered that the effects of the fires on cactus survival greatly outweigh any differences introduced by the use of unreplicated areas.

Long-term mortality

To monitor mortality, 50 plants considered alive of each of the four cactus species were randomly

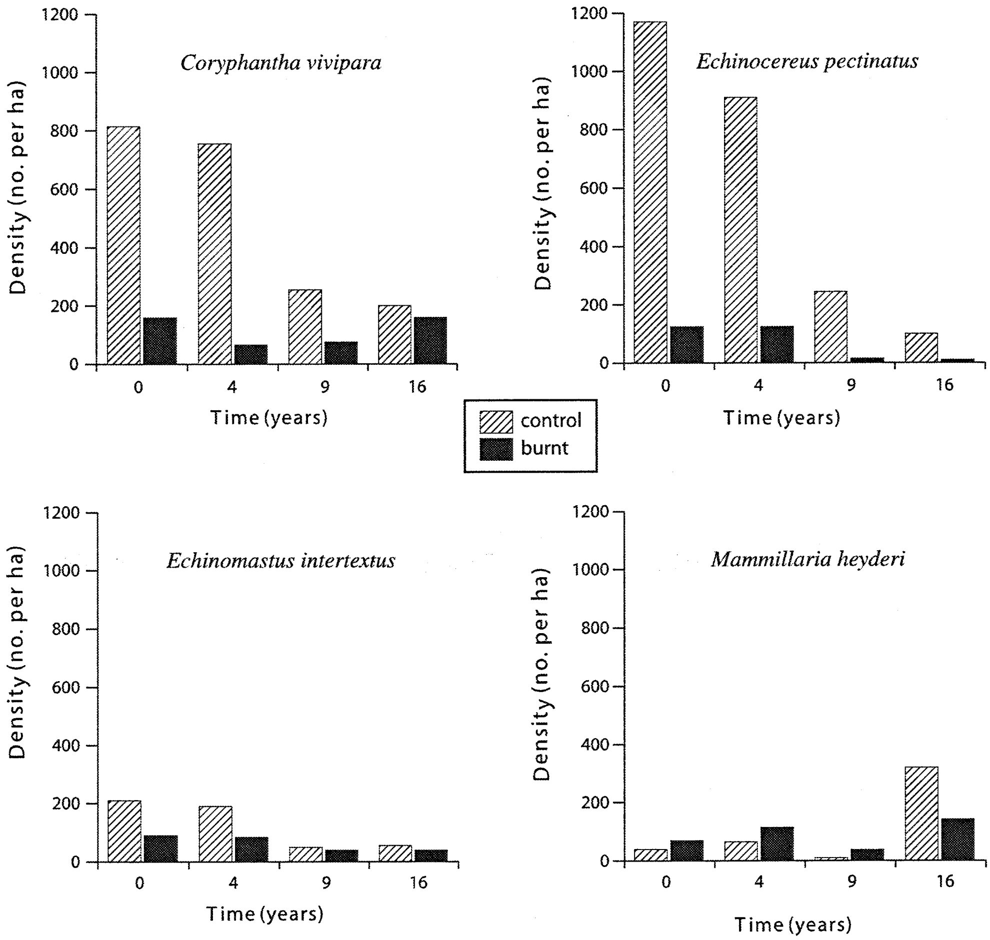

Figure 1. Density of four cacti species over time on unburnt control and burnt areas of desert grassland.

chosen on the burnt and unburnt areas (for *M. heyderi* only 24 control, unburnt plants were found). Walks along random compass angles were made through the areas to select plants. Individuals that were scorched and intact were counted as alive since Thomas and Goodson (1992) have shown that such plants are almost certainly capable of regrowth; plants were discarded as dead only when the plant body was broken from the ground or completely withered and charred. No account was taken of size when selecting plants (see Table 2 for size ranges in the four species) and plants as small as 0.5 cm tall were marked.

Plants were marked by an individually numbered aluminium tag (3.5 cm in diameter, held on the soil surface by a 5.5 cm aluminium nail), 50 cm high flags and detailed mapping. Mortality was re-estimated 8 months after the July fire (after the first winter) and then 1, 4, 9 and 16 years after the fires. On the last occasion, a metal detector was used to help locate tags buried beneath soil and litter.

Wildfire burnt over all three areas on 30 April 2002, 18 months before the final data collection. This fire had little discernable affect on the long-term mortality data, however, since previous experience (e.g. Thomas and Goodson 1992) has shown that plants killed by this fire would still have been visible as shrivelled husks or, at worst, a root collar.

Survival curves over 16 years for each species (Table 3) were prepared from the data in Table 2. Differences in survival between the burnt and control cacti within each species were estimated using the Mantel-Cox estimate of the hazard ratio, and the significance of the hazard ratios were tested using the Mantel-Cox chi-squared test (Kirkwood and Sterne 2003).

Density and growth

Density of the four species over the three areas were determined by counting all plants in detailed searches (as part of looking for the marked plants) of a subsection of the May burnt site (3366 m^2), July burnt site (4074 m^2) and the control site (3273 m^2). This was repeated at the onset (year 0) and at 4, 9 and 16 years. Estimates of cactus growth rates in the field are comparatively rare, so the height and diameter (not including spine length) of marked plants and of all plants of the four species encountered during the surveys were measured.

Results

Mortality

At the end of the study, all but four of the numbered discs were refound with the metal detector. In these four cases no live or dead remains were found within a metre radius of the estimated position and the plants were assumed to be dead. All other marked plants were dead (Table 1). At intermediate dates when mortality was re-estimated, up to 3 plants per species on an area could not be found because the numbered disc was buried by litter or soil. This resulted in variation of up to 6% in mortality depending on whether the plants were assumed to be alive or dead. To be conservative, the smallest differences between burnt and unburnt plants (shown in bold in Table 1) were used in statistical testing.

Mortality was total over the 16 years, regardless of whether plants were burnt or unburnt. Generally, however, mortality occurred more rapidly amongst burnt plants. Significantly higher mortality amongst burnt plants was seen after 8 months in *Echinomastus intertextus* (i.e. after the summer and winter rains), 1 year in *Echinocereus pectinatus* and 4 years in *Coryphantha vivipara*; and yet by 4 years in *E. intertextus* and 9 years in the other two, mortality in control plants had caught up and was not significantly different. In *Mammillaria heyderi* the pattern was different in that mortality was more rapid amongst control plants such that 4 years after the fire, mortality in control plants was three times higher than in burnt plants.

The survival curves for the four species (Figure 2), calculated from the data in Table 1, illustrate the more rapid mortality of the burnt plants in all but *M. heyderi*. The hazard ratios (HR) indicate that the average rate of mortality of burnt plants was 10.2 times that of unburnt control plants in *E. pectinatus*, 3.7 times in *C. vivipara* and 1.5 times in *E. intertextus* (all significant at $p < 0.001$). Conversely, in *M. heyderi* the average rate of mortality of burnt plants was a quarter that of control plants (significant at $p < 0.001$).

At the end of 4 years there were very few visible signs of the fires. Fire damage to surviving cacti was usually hidden due to shrinkage of the scorched tissue to a grey-coloured, tough and spineless scar tissue which was overshadowed by new apical growth. The burnt body was largely inconspicuous after four years. *M. heyderi* when burnt usually

Table 1. Mortality of marked cacti over time after the initial mortality.

Species	Treatment	Mortality of marked plants (%)					
		Time since 1987 fires (years)					*n*
		8 months	1 years	4 years	9 years	16 years	
C. vivipara	Burnt	**8**–10	**12**–14	**82**–86**	**92**–94	100	50
	Unburnt	**2**	2–**4**	36–**38**	70–**74**	100	50
E. pectinatus	Burnt	**16**	**28***	**84****	**100**	100	50
	Unburnt	**4**	**6**	16–**22**	90–**96**	100	50
E. intertextus	Burnt	**40**–44**	**44**–48*	**78**–82	86–**90**	100	50
	Unburnt	**6**	**18**	70–**72**	**96**–98	100	50
M. heyderi	Burnt	**2**	4–**6**	14–**20****	50–**56**	100	50
	Unburnt	**9**	**22**	**75**–80	**83**–88	100	24

Where two estimates are given this reflects whether plants not refound are assumed to be alive or dead. The values shown in bold were used in statistical analysis. *Notes*: Significant differences between burnt and unburnt pairs within a species (chi-squared with Yates correction for continuity using original count data) are indicated as follows: $^{*}p < 0.05$, $^{**}p < 0.001$.

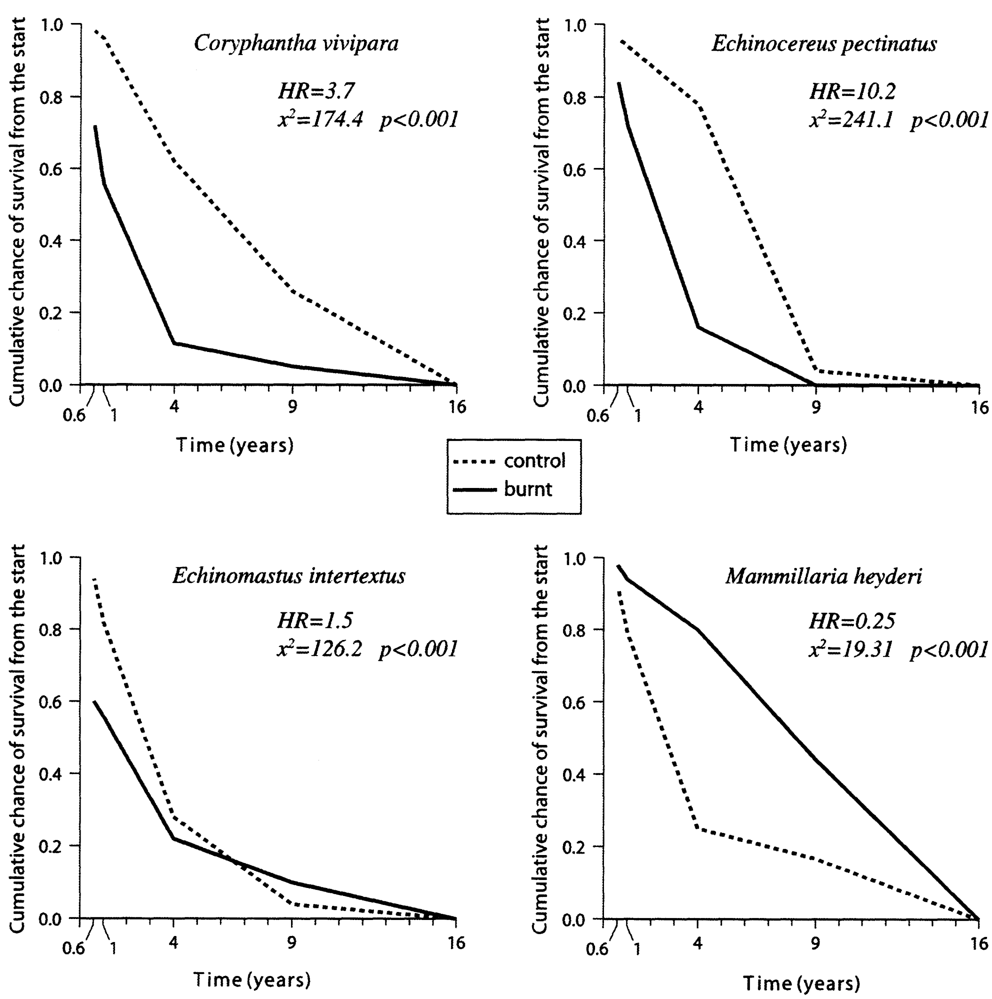

Figure 2. Cumulative chance of survival against time for four species of cacti on unburnt control and burnt areas of desert grassland. The Mantel-Cox estimate of the hazard ratio (HR) gives an indication of relative mortality rates between cacti on control and burnt areas; the significance of the ratio is indicated by the Mantel-Cox χ^2 test.

had brown and withered tubercles around the edge of flattened body but again these were not visible after 4 years. Occasional charred twigs or grass-culms could be found after 4 years but 71% of the burnt cacti and 48% of the unburnt ones that had died had either completely disappeared or were represented by just a few spines on the ground. Even fewer remains or evidence of fire were seen after 9 and 16 years. If the position of the original plants had not been marked their existence would have been impossible to discern at the end of the study. Cause of death was not easy to pinpoint because so few dead remains were found. Only two plants were found with herbivore damage (one each of *C. vivipara* and *E. pectinatus*, both burnt).

There is evidence that smaller plants were initially better at surviving fire. Four years post-fire, burnt *C. vivipara* and *E. intertextus* plants that were still alive had been significantly shorter at the time of the fire – 4.1 ± 0.64 cm (7) and 4.7 ± 0.51 cm (9), respectively; mean ± SE (n) – than those that died – 6.3 ± 0.35 cm (40) and 7.1 ± 0.48 cm (39), respectively (*t*-tests, $p < 0.05$). This may relate to flame height, especially since *M. heyderi* were uniformly short (< 3 cm) and burnt plants showed low mortality. However, *E. pectinatus* were not significantly different in initial height to *C. vivipara* or *E. intertextus* and showed no size related mortality. This size trend had disappeared by 9 years post-fire when very few plants were still alive. Survival of unburnt plants was independent of initial size at all survey times.

Size of plants and growth

Growth rates of the four species were calculated from re-measurement of the marked plants while the sizes of plants in the wider populations at the beginning and end of the study (Table 2) were estimated from measurement of all plants found.

Growth rates of individual unburnt plants were determined from repeat measurements of the marked plants. Only those plants that survived till 4 years with no apical damage were used (after that, too few plants survived for meaningful data). In 4 years, *Echinomastus intertextus* and *Coryphantha vivipara* grew in height by 3.0 ± 1.00 cm (12) and 3.0 ± 0.65 cm (10), respectively, while *Echinocereus pectinatus* grew 6.0 ± 0.70 cm (34); mean $\pm$ 95% confidence limit (n). These compare with plant heights at the beginning of the study of 5.5 ± 0.32 (50) – a 55% increase – in *E. intertextus*, 4.1 ± 0.24 (50) – a 73% increase – in *C. vivipara* and 7.1 ± 0.46 (50) – an 85% increase – in *E. pectinatus*. *Mammillaria heyderi* height growth was small and variable, 1.2 ± 2.8 cm (4) reflecting the partly underground stem. A better reflection of growth in this species is the diameter of the plate-like flat top: 3.7 ± 5.20 cm (4) in 4 years. This compares with an average diameter at the beginning of the study of 6.5 ± 3.31 (24), a 57% increase.

Increase in height of marked burnt plants over the 4 years was significantly less than of unburnt plants in all species except *M. heyderi*, undoubtedly because new apical growth was countered by shrinkage of the burnt portion; in *M. heyderi* the flat top was less damaged by fire and so less affected. Shrinkage is illustrated by the six *E. pectinatus* plants to survive over 4 years: in this species new apical growth was very distinct from the scorched pre-fire body. The burnt bodies shrunk in height by a mean of 2.4 cm to 50% of their original height so although the new post-fire growth of 4–5 cm was the same as on the unburnt plants (*t*-test, not significant at $p < 0.05$) the burnt plants were shorter than the unburnt ones.

Size of the cacti in the wider populations (i.e. not just those plants marked) at the start in July 1987 was remarkably similar to those plants found in the same areas 16 years later in October 2003. The modal height of *C. vivipara* and *E. intertextus*, and the modal diameter of *M. heyderi* were within 2 cm of each other at the two dates (Table 2). *E. pectinatus* showed a similar closeness in height on the unburnt control areas but the modal height of the five individuals found on burnt sites in 2003 were four times the height of those seen in 1987. The size of the cacti in 2003 seems to have been little affected by having been burnt by the wildfire18 months previously. The size ranges (Table 2), however, show that the populations were not identical in size distribution; the populations in 1987 had a greater number of bigger plants, suggesting that they included a proportion of older plants not found in the 2003 populations. By contrast, in 2003 there were a greater number of larger *E. pectinatus* plants than in 1987.

Density

At the beginning of the study, the density of *Coryphantha vivipara* and *Echinocereus pectinatus*

Table 2. Size of all cacti (cm) found in the study areas at the beginning of the study in July 1987, and 16 years later in October 2003.

Species	Treatment	July 1987			October 2003		
		Mode	Range	*n*	Mode	Range	*n*
C. vivipara	Burnt	5	1–12	138	4	1.5–7.5	74
	Unburnt	3	0.5–11	148	4	1–8.5	65
E. pectinatus	Burnt	3	2–15	48	12	10–17	5
	Unburnt	6.5	2.5–16.5	50	6	1.5–21	28
E. intertextus	Burnt	3	1–14	152	5	3–10	22
	Unburnt	4	2–15	92	2.5	2–8	19
M. heyderi	Burnt	8.5	1.5–14	49	7.5	1–9.5	97
	Unburnt	9	1.5–13	24	8.5	1.5–11.5	90

Data shown are heights except for *Mammillaria heyderi* for which diameters are shown.

was notably high on the unburnt control site (815 and 1170/ha, respectively) with all other species being below 210/ha on burnt and unburnt areas. As discussed in the Methods, this initial difference is attributed to very local variations in rainfall and seedling establishment conditions in previous years. The general trend over the study was a decline in density, particularly on the control site (Figure 1). However, the density of *Mammillaria heyderi* increased dramatically, on the burnt area by >200% and on the control area by >800% over 16 years. The density of *C. vivipara* on the burnt site declined over the first four years and then rose after 16 years to reach its initial density. These final densities may be an underestimate because some cacti were killed by the wildfire 18 months before the final recording date; their burnt remains were easily seen but since they were unmarked it was difficult to reliably identify the species. Earlier work on these species (Thomas and Goodson 1992) suggests that mortality could be as high as 10%, or much more in *Echinomastus intertextus*. Estimates from dead remains during the final survey suggest, however, that mortality in *C. vivipara* and *M. heyderi* was likely less than 10% and 5%, respectively, both on the control and burnt sites. Extra mortality from the wildfire for *E. intertextus* was probably nearer to 30%. Adding these percentages to the 2003 densities would still not bring the populations up to the 1987 densities given in Figure 1, especially on the control site (for all species: burnt site: 401 plants estimated per ha in 2003 compared to 445/ha in 1987; control site: 675/ha in 2003 compared to 2235/ha in 1987). *E. pectinatus* density fell dramatically on burnt and unburnt sites over the 16 years with no signs of recovery (Figure 1).

Discussion

The mortality of burnt plants continued beyond the first few years until all the marked plants were dead within 16 years. Surprisingly, the mortality of unburnt control plants was also total within 16 years but occurred at a slower rate; the effect of fire was therefore not so much in higher mortality but faster mortality. Thus while over the 16 years of the study, fire made no difference to the overall mortality, it did affect how rapidly plants died within that time. This was especially important in *E. pectinatus*, where the rate of mortality of burnt plants was more than 10 times that of unburnt plants, and in *M. heyderi* where the opposite occurred and the mortality rate of burnt plants was a quarter that of unburnt plants. This is significant: whereas previous studies have shown the short-term effect of fires to be small and even negligible, these results show that the long-term effects are potentially more serious and may result in significantly smaller populations of small-growing cacti.

A number of studies have demonstrated high mortality of cactus seedlings in the field (e.g. Valverde et al. 2004). It seems likely that adult plants are replaced by cohorts of seedlings recruited only during particularly favourable periods of wet weather (Gibson and Nobel 1986; Contreras and Valverde 2002). Comparing the 2003 populations (16 years post-fire) with that of the original 1987 populations, which had some larger (inferred as older) plants, it is clear that recovery was not yet complete after 16 years even in the two species whose densities had reached or exceeded pre-fire densities on the burnt site.

The main danger of fire appears to be faster removal of individuals from the population, especially in *E. pectinatus*. Since cacti have no appreciable soil seed bank this could affect the long-term viability of populations by removing seed producing plants before a suitable recruitment period arrives, increasing the risk of local decline in numbers and potential local extinction. This does not imply that all populations are doomed. If a good establishment year occurs within the reduced life span, high recruitment can take place as seen in *C. vivipara* and *M. heyderi* on the burnt site in this study, perhaps aided by reduced competition after fire. However, increased mortality rate and consequently a reduced life span does decrease the probability that populations will be replaced or supplemented before local extinction. Rapid mortality of cohorts, speeded up by fires, and poor recruitment may explain why some hillsides in the study area are devoid of small cacti while others, that appear identical, have a high density; it depends at what stage a particular hillside is in terms of mortality and recruitment episodes. This would explain the unexpectedly high density of *M. heyderi* on the unburnt site at the end of the study.

Looking at the wider populations rather than just the marked plants, three of the species showed a sharp dip in density on the unburnt control area over the duration of the study. Since the control site had a consistently denser growth of grass and herbs (e.g. at year 9: control 308 ± 84 g/m^2; burnt sites 200 ± 34 and 212 ± 43; mean $\pm$ SE ($n = 8$)) this may reflect higher competition for water and light. This would also explain the increase in density of the low-lying *M. heyderi* over the first four years on the burnt site, and the lower initial mortality on the burnt site. Since grassland fire temperatures typically rise rapidly up to a height of 6–15 cm where they are twice as high as at the soil surface (Wright and Bailey 1982), the low-growing *M. heyderi* would likely be less damaged by fire and benefit from reduced competition. This is somewhat at variance with Bunting et al. (1980) who observed 74% mortality of burnt *M. heyderi* after 4 years but since their study was in mixed prairie the fires were likely to be hotter. The more rapid demise of the taller three species of cacti when burnt is perhaps not surprising since cacti show no real adaptations to fire (Thomas 1991); rather they are adapted to hot arid conditions (protected apical growing point, the ability to produce basal offsets) which give them some protection against the hotter temperatures of fire.

The data presented suggests that the life-span of these four species is short and apparently less than two decades. Some of the initial marked plants were very small (Table 2) and still died in this time. Detailed mapping at each of the density surveys of the smallest plants (< 1 cm tall) showed that those found at a particular survey date were not recorded at the previous survey date. It is unlikely that every very small plant was overlooked (although experience shows that they are easily missed) but rather suggests that the smallest plants were only a few years old. Moreover, the marked plants still alive at the end of 4 years were some of the largest in the wider population suggesting a rapid turn-over of plants. Estimated growth rates of unburnt plants over the first 4 years are consistent with the largest plants found on the site in 2003 mostly having established since 1987.

These results raise a number of questions about the long-term dynamics of the cactus populations in these grasslands. If mortality, particularly of burnt plants, is so rapid and the life span so short, why has this not been widely reported before? Since signs of fire (except for deeply charred burnt trunks and posts) disappeared within 4 years, and dead plants soon disintegrated and the remains dispersed, estimates of long-term mortality would have been considerably lower if plants had not been marked. The similar sized plants in the wider populations in 1987 and 2003 give the superficial impression that nothing has changed over 16 years except that density had declined in some species, and yet in reality there was a whole new cohort of plants.

The patchiness over time of cactus establishment suggests that climate change could have significant effects: an increase in dry periods or high temperatures could reinforce the effect of fire leading to severe population reductions and even local extinction before recruitment is possible. Fire is also becoming more common in desert grasslands (Schmid and Rogers 1988) due to wildfires and increased use as a management tool. If fuel is allowed to build up to ensure successful burning (for example by a temporary reduction in grazing), such as is the case on the research ranch, then individual fires are likely to be damaging. If the desire is to return to something approaching the original fire frequency to manage for shrub encroachment (e.g. Drewa and Havstad 2001), which in these desert grasslands is around 7–10 years (McPherson 1995), and thus within the apparent normal life span of these cacti, then cacti populations will be increasingly restricted to fire-proof refugia, putting pressure on their populations.

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