LIMITATIONS TO NATURAL PRODUCTION OF *LOPHOPHORA WILLIAMSII* (CACTACEAE) III. EFFECTS OF REPEATED HARVESTING AT TWO-YEAR INTERVALS FOR SIX YEARS IN A SOUTH TEXAS (U.S.A.) POPULATION

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ABSTRACT

Here we report the 6-year results of a long-term study of the effects of harvesting on a wild population of the cactus *Lophophora williamsii* (peyote). Harvesting was performed using the best known technique: removing only the crown from the top of the plant. The two-year interval between harvests was chosen because it was similar to that observed by persons who harvest peyote for legally protected religious use by members of the Native American Church. Plants in the study were divided into three treatment groups: (1) control plants that were never harvested, (2) plants that were harvested only once, at the beginning of the study, and (3) plants that were harvested at the beginning of the study and every two years thereafter. Over the last two years of the study (2012–2014), the survival rate was significantly lower (77%) in the plants harvested every two years than in the once-harvested plants (100%) and the unharvested control plants (98%). At the end of the 6th year of the study, average volume of living crown tissue per plant was significantly and substantially lower in the plants harvested every two years than in the once-harvested plants and the unharvested controls. The average volume of once-harvested plants was 27% lower than that of the controls, although this latter difference was not statistically significant. The modal number of crowns per plant varied with treatment and over time; in the plants harvested every two years it underwent a progression from 1 to 2 to 3 to 1 in response to successive harvests. The results of this study indicate that a six-year recovery period, following the harvesting of peyote in natural habitats, is probably not long enough to ensure long-term sustainability.

Key Words: cactus conservation, peyote harvest, cactus overharvesting, Native American Church, peyote conservation status

RESUMEN

Aquí reportamos los resultados de seis años de un estudio a largo plazo sobre los efectos de cosechar individuos del cactus *Lophophora williamsii* (peyote) en una población silvestre. La cosecha se hizo utilizando la mejor técnica que se conoce, recogiendo solamente la corona de la parte superior de la planta. El intervalo de dos años entre cosechas fue similar al utilizado por personas que cosechan peyote para uso jurídicamente protegido por los miembros de la Native American Church. Las plantas en el estudio fueron divididas en tres grupos de tratamiento: (1) las plantas de control que nunca fueron cosechadas, (2) las plantas que fueron cosechadas sólo una vez, al comienzo del estudio, y (3) las plantas que fueron cosechadas al comienzo del estudio y posteriormente cada dos años. En los últimos dos años del estudio (2012–2014), la tasa de supervivencia fue significativamente menor (76,5%) en las plantas cosechadas cada dos años, que en las plantas cosechadas una sola vez (100%) y las plantas de control que no fueron cosechadas nunca (97,7%). Al final del sexto año del estudio, el volumen promedio del tejido vivo de la corona por planta fue significativamente menor en las plantas cosechadas cada dos años, que en las plantas cosechadas una sola vez y las plantas de control que nunca fueron cosechadas. El número modal de coronas por planta varió con el tratamiento y con el tiempo; en las plantas cosechadas cada dos años hubo una progresión desde 1 a 2 a 3 a 1 en respuesta a las cosechas sucesivas. Los resultados de este estudio indican que un período de recuperación de seis años después de la recolección del peyote en el hábitat probablemente no es suficientemente largo como para asegurar la sostenibilidad a largo plazo.

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INTRODUCTION

Lophophora williamsii (Lem. ex Salm-Dyck) J.M. Coult. (Cactaceae), commonly known as peyote, is a small globular cactus of northeastern Mexico and adjacent border areas of Texas. The crowns (apical chlorophyllous portions of the stem) of these plants are approximately hemispherical in shape and generally protrude a few cm above ground level. Some plants are caespitose, i.e., they have multiple crowns arising from a single nonchlorophyllous (generally subterranean) stem. What was known of the biology of this species up to the mid-1990s is summarized by Anderson (1996). Early suggestions that the species might be threatened by overharvesting came from Morgan (1976), Anderson (1995), and Trout (1997).

The harvested crowns of peyote are collected and sold by licensed distributors to the Native American Church (NAC) for religious use as protected by U.S. law. The anatomy of harvesting and the process of regeneration of new crowns in response to harvesting are described by Terry and Mauseth (2006). It is now abundantly clear that the current rate of harvesting of peyote from wild populations is not sustainable (IUCN 2013; NatureServe 2012; Terry et al. 2011, 2012). In March 2008 we began the first experimental investigation of the effects of harvesting on peyote plants in situ. In previous papers we reported the effects that were detectable two years (Terry et al. 2011) and four years (Terry et al. 2012) after the initial harvest. The present report focuses on effects detectable six years after the initial harvest, in once-harvested plants and/or in plants harvested every two years, the latter treatment representing the harvest frequency observed by persons who harvest peyote for legally protected religious use by members of the Native American Church.

MATERIALS AND METHODS

The study site in the Tamaulipan thornscrub of South Texas was described previously by Terry et al. (2011). The study design was described in detail by Terry et al. (2012). In summary, there were three treatment groups: (1) a group of 50 plants which were unharvested control plants; (2) a group of 25 plants which were harvested only once, at the beginning of the study; (3) a group of 25 plants which were harvested at the beginning of the study and reharvested every two years thereafter. All plants were harvested using the best known technique, removing only the crown from the top of the plant with a sharp knife. All plants in the study were individually numbered and tagged in situ, along a transect through the population. Data collected on each plant at each census (0, 2, 4 and 6 years) included number of crowns, number of ribs on each crown, and diameters of the crowns. All statistical analyses were done with SAS 9.3 (SAS Institute, Cary, NC, USA).

Statistical analyses of survival.—Because a census of plants was conducted every two years (2008, 2010, 2012, 2014), each census interval was two years long. Harvesting was done directly after each census, and therefore survival rates reflect the effects of treatments of preceding years, but not of the treatment of the census year. Survival rates were calculated for each census interval separately. Only plants present at the beginning of the given interval (and not dug up by feral hogs during the interval) were used to calculate survival rates. Four plants were dug up by hogs during the first interval and were therefore dropped from all survival calculations, and one plant was dug up during the third interval and was therefore dropped from the calculation of survival rate during the third interval. Figure 1 is not an exact representation of cumulative survival rates (which would have been affected by hog-caused mortality), but instead shows the products of the calculated interval survival rates for each treatment (e.g., the proportion of plants surviving to census 3 is the product of the survival rate from census 1 to census 2, times the survival rate from census 2 to census 3).

A single survival rate was calculated for harvested plants for the first census interval (2008–2010), because both groups of harvested plants were harvested after the first census. The “plants harvested once” were not harvested again. Plants harvested once and plants harvested multiple times were separated in the analyses of survival during the second (2010–2012) and the third (2012–2014) census intervals. Fisher’s exact test was used to compare treatments within each of the three census intervals, because the expected values of some cells were < 5, making ordinary χ^2 tests inappropriate.

Statistical analyses of size.—Our primary measure of plant size was estimated total above-ground volume. It

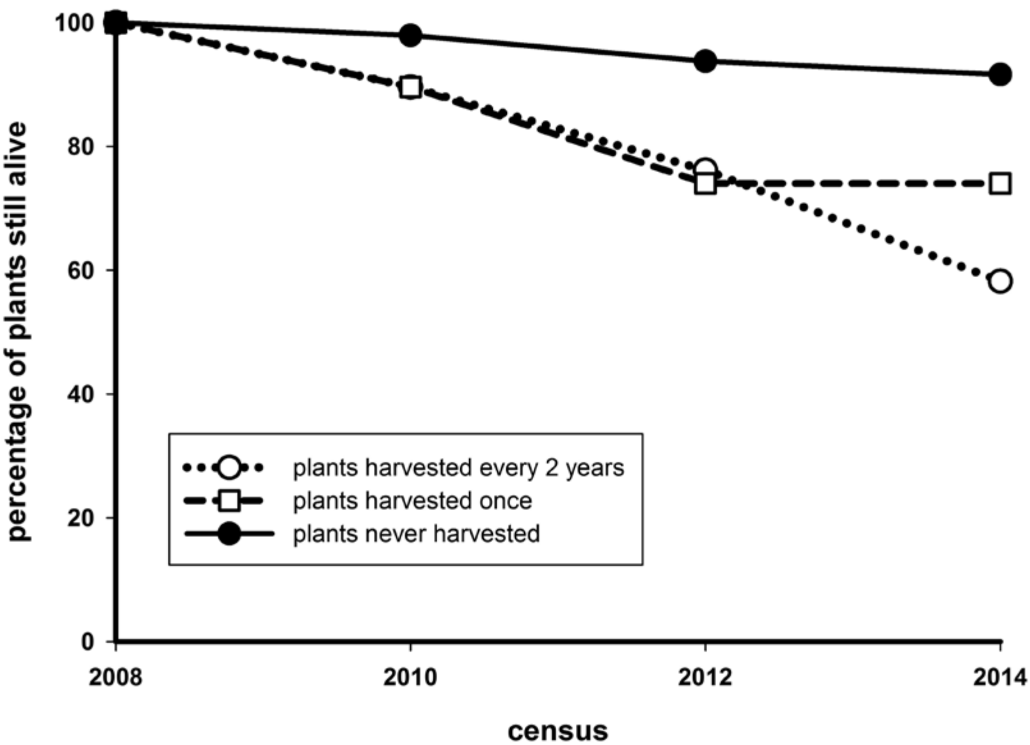

Fig. 1. Cumulative proportions of plants remaining alive after excluding plants dug up by hogs from the calculations (see Methods). Plants were harvested immediately after each census. Plants harvested once were harvested only after the first census (2008). For statistical tests, see Table 1.

was calculated from the diameter of each crown by assuming that each crown was a hemisphere: estimated crown volume = ⅔ π (crown diameter/2)^3. If a plant had multiple crowns in a given census, the estimated volumes of all of its crowns were summed to obtain estimated total above-ground volume of that plant. As is usual with plant size measurements, the distribution of volume was skewed, with a right tail (i.e., a few large plants, more smaller plants). No single transformation of total volume produced residuals that met the assumptions of analysis of variance for all years. Instead, volumes from censuses in 2008 and 2012 were square-root transformed before analysis, and volumes from censuses in 2010 and 2014 were log-transformed before analysis. (The log-transformation over-corrected skewness in the censuses of 2008 and 2012; the square-root transformation under-corrected it in the censuses in 2010 and 2014). Treatments were then compared with analysis of variance (ANOVA). If the effect of treatment was significant and there were >2 treatments to be compared, individual treatments were compared, using the Tukey adjustment for multiple testing. For graphical presentation (Fig. 2), the mean, mean plus 1 standard error, and mean minus 1 standard error of each treatment were separately back-transformed with the appropriate function, using the standard error of each treatment from the corresponding ANOVA.

Another measure of size is the number of crowns per plant. When the experiment was initiated, each experimental plant included in the groups to be harvested had exactly one crown. That constraint was not imposed on the control plants, however, and the few multi-crowned individuals that occurred along the study transect were not rejected from inclusion in the control group. This was done in order to ensure that the control group was representative of the population in terms of the full range of crown numbers per individual plant. The number of crowns/plant in each subsequent census was found to be Poisson distributed, and treatments each year were therefore compared with a generalized linear model with a Poisson distribution for which the

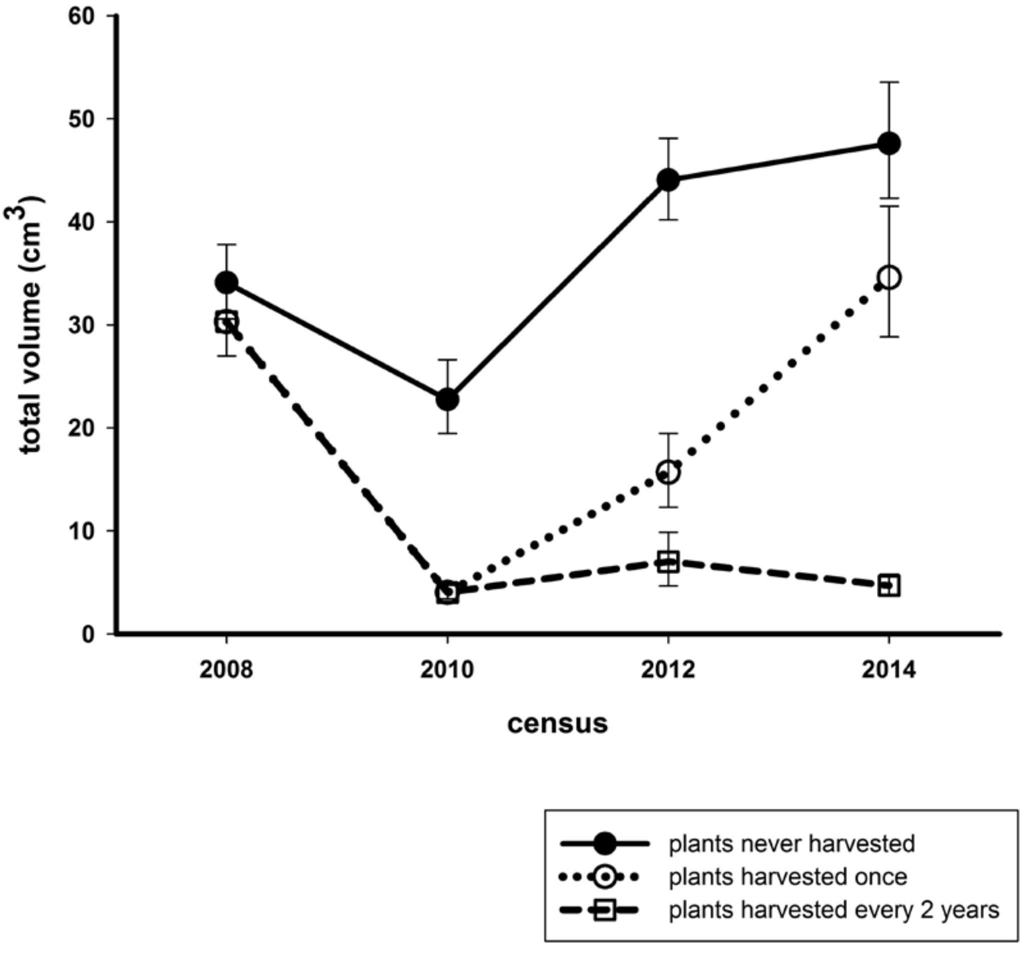

Fig. 2. Plant size, measured as total above-ground volume. Points represent back-transformed means; error bars are means ± 1 standard error, separately back-transformed.

log is the link function. To supplement this analysis, we also calculated the change in number of crowns of each surviving plant during each of the last two census intervals, and compared the distributions of size changes among treatments with Fisher's exact test.

RESULTS

Survival.—Survival rates of control plants remained high: more than 95% in each two-year census interval (Table 1, Fig. 1). Survival rates of plants harvested every two years were consistently lower than those of control plants, and decreased over time; the rate at which these plants survived the third census interval, by which time they had been harvested three times, was only 77%. There is evidence that the negative effect of harvesting on survival lasts more than two years: survival rates of once-harvested plants did not return to control levels until four years had passed after they were harvested (i.e., until the third census interval, 2012–2014).

Size.—The once-harvested plants appeared to continue to be in the process of recovering from the adverse effects of being harvested six years before (Table 2, Fig. 2). Six years after harvesting, we no longer were able to detect a significant difference in size (total above-ground volume) between never-harvested and once-harvested

TABLE 1. Survival rates during each census interval. Plants were harvested immediately after each census; plants harvested once were harvested only after the first census. NS, not significant.

	2008–2010	**2010–2012**	**2012–2014**
control plants	97.9%	95.7%	97.7%
plants harvested once	89.6%	82.6%	100%
plants harvested every two years	89.6%	85%	76.5%
	NS	$P = 0.013$	$P = 0.0097$
sample size	N = 96	N = 89	N = 80

TABLE 2. Results of ANOVAs comparing plant volumes among treatments. All harvests took place immediately after the census in the calendar year indicated. Analyses for census years 2008 and 2010 compare unharvested and harvested plants; the first harvest (2008) occurred after the first census. Analyses for census years 2012 and 2014 compare unharvested plants, plants harvested once (after the 2008 census), and plants harvested every two years (i.e., after the censuses of 2008, 2010, and 2012). Control, never harvested; once, harvested once after the first census; multi, harvested every two years after each census.

census year	**transformation used**	***F***	$P_{treatment}$	**multiple comparisons**		
				control v once	control v multi	once v multi
2008	square root	$F_{1,98} = 0.59$	NS	—[a]	—[a]	—[a]
2010	log	$F_{1,88} = 58.31$	< 0.0001	—[a]	—[a]	—[a]
2012	square root	$F_{2,76} = 28.73$	< 0.0001	<0.0001	<0.0001	0.13
2014	log	$F_{2,71} = 45.29$	< 0.0001	0.31	<0.0001	<0.0001

[a] no multiple comparisons needed; treatment *P* value compares control and harvested plants

plants. This of course does not mean that the once-harvested plants had completely recovered, especially given that small sample sizes reduced the power of our test. A power analysis of our results indicates that, given the average control plant size of 48 cm^3 in the 2014 census and the observed distribution of plant sizes in that census, we could have detected a significant difference between the control and the once-harvested plants only if the once-harvested plants had been < 28 cm^3 in size on average (42% smaller); in fact, they were 35 cm^3 in size on average (only 27% smaller). In contrast, the plants harvested every two years remained very small. We were not able to detect a temporal trend in the volume of those plants, perhaps because very small plants simply died.

As the experiment proceeded, the distribution of crown numbers in control (i.e., never harvested) plants remained quite constant (Figs. 3 and 4), with the average number of crowns per control plant remaining close to 1.7 (Table 3). The majority of control plants always had one crown, but note the long right tails of the distributions in Fig. 3, each of which includes a few control plants with five or more crowns each.

The first harvest (2008) caused a significant increase in the number of crowns per harvested plant, with a modal value of 2 crowns per plant and a mean of 2.58 (Table 3, Fig. 3). (However, these new crowns were quite small; recall that harvesting reduced average plant volume substantially). Over the next four years plants that were not re-harvested continued to have a modal value of 2 crowns per plant, with little change in their distribution (Figs. 3 and 4).

The second harvest of plants harvested every two years shifted the modal value to 3 crowns per plant (mean 2.56) in 2012, which was more crowns/plant than the once-harvested plants in the same census had (mode 2, mean 2.16 crowns/plant) (Table 3; Fig. 3, census 2012). However, 31% (5 of 16) of plants harvested every two years decreased in crown number during this period (Fig. 4, 2010–2012). The statistical test comparing crown number distributions among treatments in 2012 did not quite reach significance (Table 3: $P = 0.09$), nor did the statistical test comparing changes in crown number ($P = 0.18$).

The third harvest of plants harvested every two years reduced the average number of crowns per plant in 2014, and one crown per plant was once again the most common value in these plants (Fig. 3, census 2014,

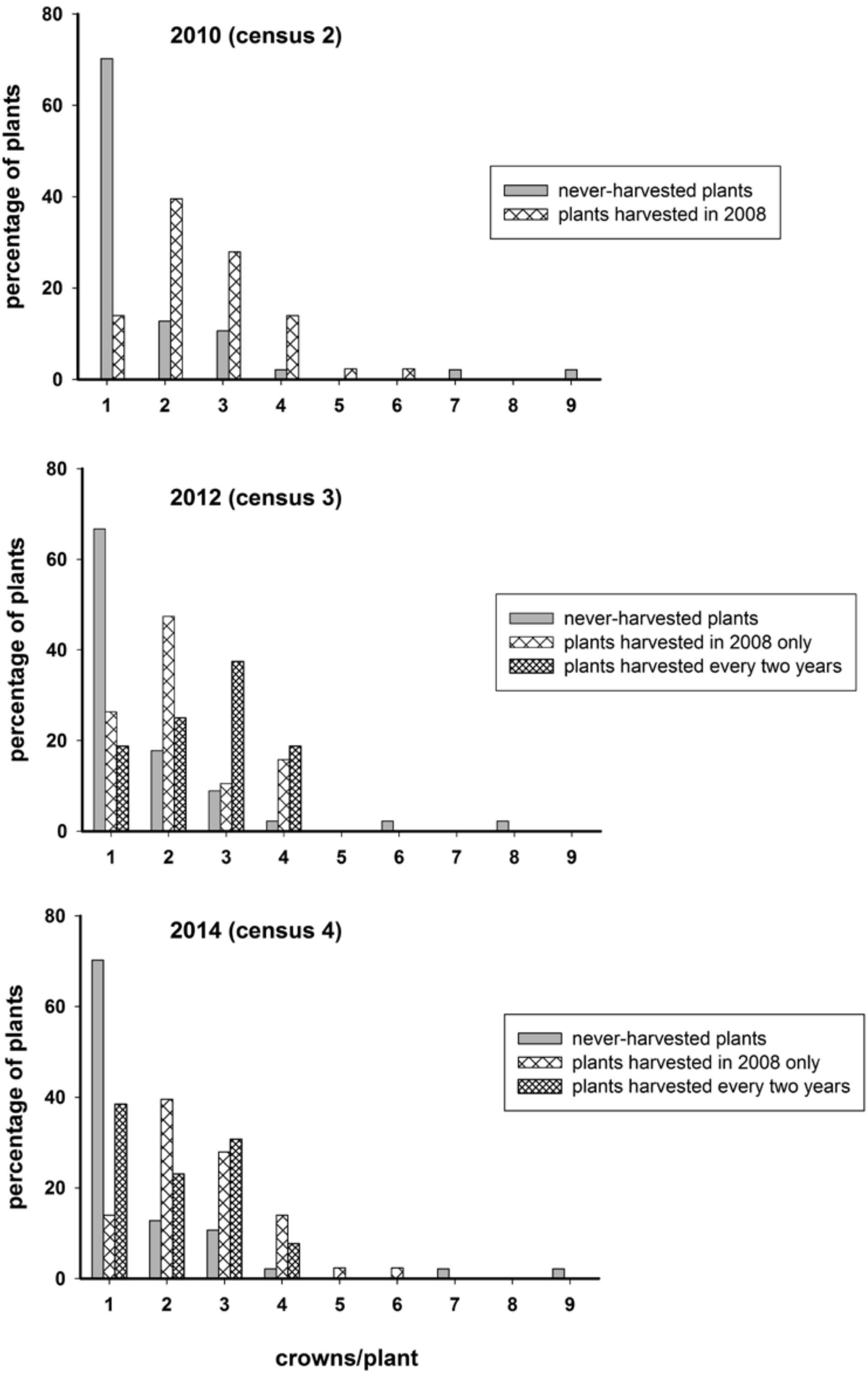

Fig. 3. Distributions of numbers of crowns per plant. For statistical tests, see Table 3.

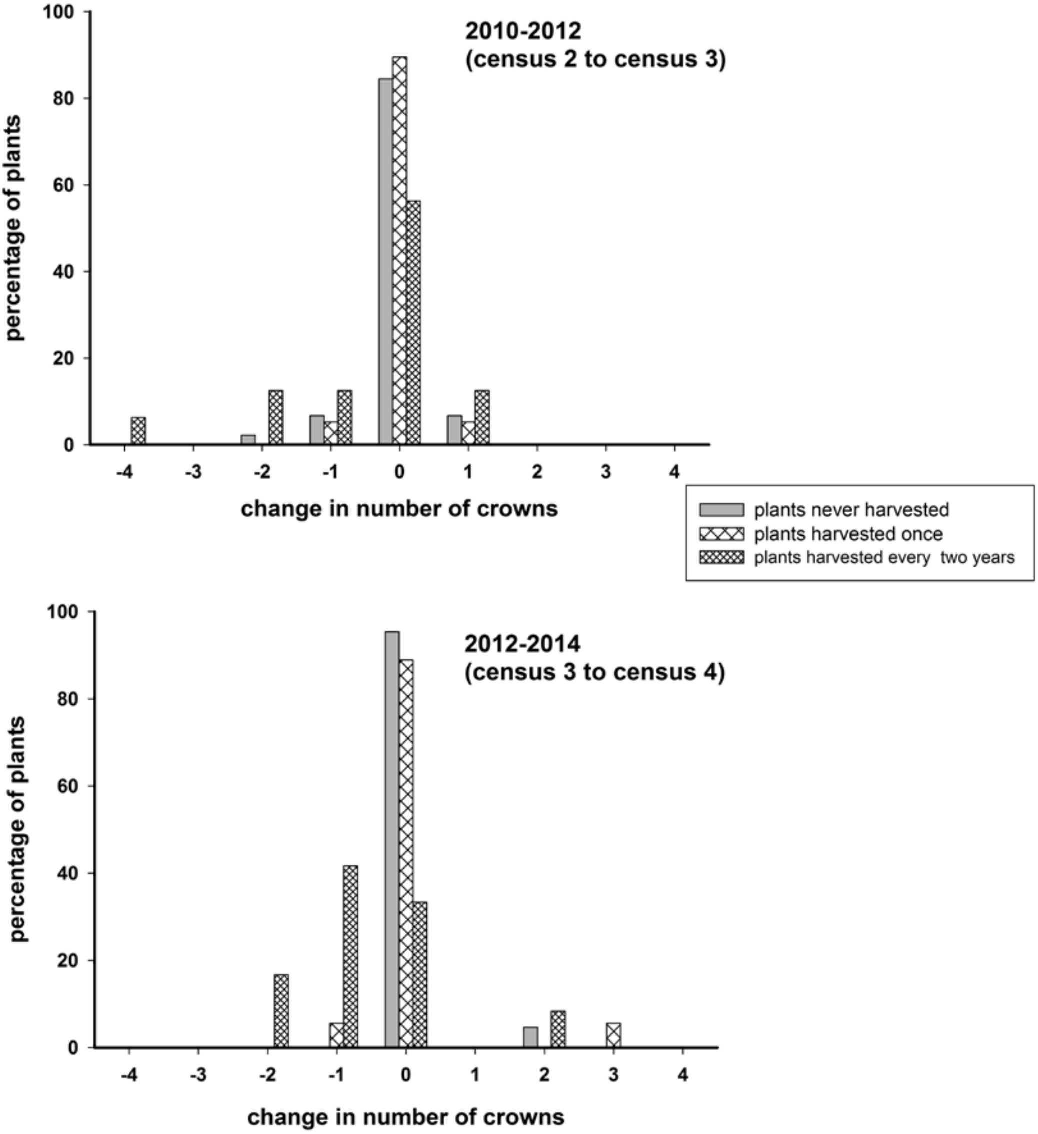

Fig. 4. Distributions of changes in the number of crowns per plant.

plants harvested every two years). Of plants harvested every two years, 58% (7 of 12) had fewer crowns at the end of this census interval (2014) than they did at its beginning (2012) (Fig. 4, 2012–2014, plants harvested every two years). While the differences in crown number among treatments did not reach statistical significance in 2014 (Table 2: $P = 0.31$), the statistical comparison of the changes in crown number (Fig. 4, 2012–2014) among treatments was highly significant ($P < 0.0001$).

DISCUSSION

During the fifth and sixth years of this ongoing experimental study of a peyote population, we saw few changes in the behavior of never-harvested (control) plants. Once-harvested plants continued to recover from harvesting, but plants harvested every two years continued to experience lowered survival rates and to be quite

Table 3. Numbers of crowns per plant.

	comparison of treatments		average no. of crowns/plant
	F (df)	P	
census year 2010	8.06 (1,88)	0.006	
control			1.70
harvested			2.58
census year 2012	2.46 (2,77)	0.09	
control			1.69
once-harvested			2.16
harvested every 2 yrs			2.56
census year 2014	1.19 (2,71)	0.31	
control			1.74
once-harvested			2.33
harvested every 2 yrs			2.08

small, but for the first time also showed a reduced capacity to produce new crowns. The survival rate and individual sizes of never-harvested plants indicate that the site continued to be suitable for this species. However, the loss of plants to digging, apparently by feral hogs, did not cease; it continued to be a concern.

Effects of harvesting.—The recovery of once-harvested plants from their harvest in 2008 appeared to be nearly complete in terms of survival: their survival from 2012 to 2014 was not different from that of the never-harvested plants. This delayed but marked increase in the survival rate of the once-harvested group attests to the resilience of the species when it is allowed a long enough respite from further harvesting. But note that this recovery was delayed and occurred only in the third two-year period after harvesting; harvesting reduced survival for at least four years.

By our best measure of size, the estimated above-ground volume of each plant, the once-harvested plants also continued to recover in terms of size (Fig. 2). However, inspection of Fig. 2 suggests that this recovery was not yet complete in 2014. Although the difference in size between never-harvested and once-harvested plants was no longer significant in 2014, this does not mean that the two groups did not differ. A power analysis of our data indicated that, due to plant-to-plant variability and small sample sizes, only differences of 42% or more from average control plant size would have been detected as statistically significant. In other words, the relatively low power of the analysis made a type II error (false negative, i.e., failure to reject the null hypothesis) very likely as soon as the once-harvested plants were about half the size of the never-harvested plants. If we had been able to design the study with a total of 500 plants instead of 100 (which would have implied finding a landowner who was willing to allow 250 peyote plants to be harvested from his property), we would have had substantially greater statistical power, which might well have resulted in a *P* value less than 0.05 for the comparison of control and once-harvested plants. The pattern evident in Fig. 2, these statistical considerations, and the precautionary principle, strongly support the assumption that **six years is not long enough to wait** after a population of peyote is harvested before going back and re-harvesting the population, if the goal is a sustainable regimen of harvesting.

In contrast to the ongoing recovery of once-harvested plants, the plants harvested every two years continued to die at significantly higher rates during 2012–2104, and the survivors remained extremely small. All evidence continues to support the conclusion that harvesting this species every two years, even using best-practice harvesting methods, is not sustainable.

Can the increase in crown number compensate for the negative effects of harvesting?—If the death of one crown on a plant is independent of the death of another crown on the same plant, then having more crowns would increase the plant's chance of survival. It is not clear what mechanisms would create this scenario, because both resource competition and herbivory likely affect all the crowns of a plant at once. However, it is possible that this scenario was in part the reason that the survival rate of once-harvested plants recovered from harvesting before their volume did. In any case, the multiple crowns of the repeatedly-harvested plants did not prevent their survival rate from remaining lower than that of control plants.

By 2014 the number of crowns of the repeatedly-harvested plants had declined from its peak in 2012, while the above-ground volume of these plants remained extremely low. It seems likely that these repeatedly-harvested plants had exhausted most of their stored resources by 2014 and therefore their ability to regrow following harvest was reduced. Presumably each harvest used up stored carbohydrates and other resources, as well as reducing the length of time during which the plant could accumulate new resources via photosynthesis. Viable areoles on the nonchlorophyllous/subterranean portion of the stem are probably also depleted by repeated regrowth after harvesting. Such areoles are not replaced, as they are generated early in the life of the plant at the apical meristem and migrate radially as the plant grows, ultimately becoming incorporated into the basal (non-chlorophyllous) portion of the stem, below the crown. Once such an areole is used up in producing regrowth in the form of an axillary branch with its new crown, that areole is permanently extinguished by the harvesting of that crown.

Management implications.—The continuing decline of the plants harvested every two years clearly and strongly supports not harvesting wild-grown peyote plants this frequently. As we argued in a previous paper (Terry et al. 2012), frequent harvests are producing a classic case of the overharvesting of a wild population.

We also conclude that even six years is probably not long enough for plants to recover from harvesting, even using best-practice harvesting methods (clean knife cut, leaving the non-chlorophyllous stem and roots intact). It is possible that eight years between harvests would allow recovery; we do not have data to address this hypothesis as yet. However, for the purpose of considering conservation options, let us make the assumption that eight years would be sufficient for plants to completely recover from a single harvest of their crowns by the current best-practice method. We have heard several objections to the proposition that cultivation of peyote is the single most viable solution to the current problem of reduced availability of peyote. One of the most frequently heard objections is that "10 years is too long" to wait for peyote planted from seed to reach maturity in a greenhouse so that it would be available for harvesting for ceremonial use by the Native American Church. But if that 10-year waiting period for sustainable production of cultivated peyote is now compared to an 8-year waiting period required for sustainable production of peyote in its natural habitat, perhaps the 10-year wait for greenhouse cultivation to come on line to allow adequate annual production for the Church's ceremonial needs is not so unreasonable after all. A greenhouse-grown supply of peyote would also eliminate all the uncertainty of relying on collection from the wild and greatly reduce the real possibility that this species will soon become commercially extinct in the wild, that is, so rare that it is no longer economically feasible to collect wild plants.

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