LIMITATIONS TO NATURAL PRODUCTION OF *LOPHOPHORA WILLIAMSII* (CACTACEAE) I. REGROWTH AND SURVIVORSHIP TWO YEARS POST HARVEST IN A SOUTH TEXAS POPULATION

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ABSTRACT

Lophophora williamsii (peyote) is a cactus whose crowns are commercially harvested for religious use as an ingested psychoactive sacrament by members of the Native American Church. Over the past quarter century peyote has become progressively less available, due in part to improper harvesting techniques and excessive harvesting. Since anatomical aspects of the regrowth of peyote and best harvesting practices were explicated in a previous study (Terry & Mauseth 2006), the principal focus in the present study was to determine the effects of harvesting where only best practices were employed. We assessed the effects of (1) harvesting per se (a single harvesting event evaluated after two years), (2) repeated harvesting (two harvesting events two years apart), and (3) not harvesting at all. After two years, the once-harvested group had a 90% survival rate and the unharvested control group had a 98% survival rate, a difference that was not statistically significant. The above-ground volume of the unharvested plants was significantly larger than that of the regrown harvested plants. While the regrown harvested plants had on average more crowns, their crowns were significantly smaller, in comparison to those of the unharvested plants. After two years, the surviving plants in the harvested group were divided into two subgroups, one of which was harvested for a second time. The other subgroup consisted of plants that had been harvested only once (at the start of the study) and were not reharvested. The weights of the crowns obtained in the second harvest were significantly lower than the weights of the crowns obtained in the first harvest from the same plants two years earlier. The net effect of a single harvesting was a reduction of plant above-ground volume by almost 80% after two years of regrowth. These data reflect what is occurring on a massive scale in habitat where peyote is commercially harvested. The annual numbers of crowns being harvested have not yet decreased drastically, due to the increased number of crowns produced as regrowth in response to harvesting. But the average size of the crowns in the regulated peyote market has decreased markedly due to too-early harvesting of immature regrowth crowns. These results—with emphasis on the conspicuous reduction in mean size of individuals—are typical of overharvested populations of wild-collected species, such as ginseng. The conclusion for conservation management is that reducing the frequency of harvesting of wild peyote would allow regrowth crowns to mature in size—thus reducing the number of crowns per dose required for sacramental consumption. It would also allow regrowth crowns to mature sexually, which would effectively de-suppress the production of seed for the next generation.

RESUMEN

Lophophora williamsii (peyote) es una cactácea, cuyos tallos se cosechan comercialmente para uso religioso como un sacramento psicoactivo ingerido por miembros de la Native American Church. En el último cuarto de siglo, el peyote se ha hecho progresivamente menos disponible, debido por una parte al uso de técnicas inapropiadas de cosecha y por otra a la práctica de cosechar en exceso. Ya que los aspectos anatómicos del recrecimiento del peyote y las mejores prácticas de cosecharlo fueron explicados en un estudio previo (Terry y Mauseth 2006), el enfoque principal en el estudio presente era determinar los efectos de cosechar utilizando solamente las mejores prácticas. Evaluamos los efectos de (1) cosechar de por sí (un solo evento de cosechar evaluado después de dos años), (2) cosechar repetidamente (dos eventos de cosechar, el segundo dos años después del primero), y (3) no cosechar. Después de los dos años, el grupo cosechado una sola vez mostró una tasa de supervivencia de un 90% y el grupo no cosechado mostró una tasa de supervivencia de un 98%, tal diferencia no fue estadísticamente significativa. El tamaño de la porción por encima del suelo de las plantas del grupo control fue significativamente mayor que el de las plantas que volvieron a crecer después de la cosecha. Mientras que las plantas cosechadas y vueltas a crecer tuvieron más coronas en el promedio, sus coronas fueron más pequeñas que las del grupo no cosechado—ambas diferencias fueron también significativas.

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Después de los dos años, las plantas supervivientes en el grupo cosechado fueron divididas en dos subgrupos, uno de los cuales fue cosechado por segunda vez. El otro subgrupo consistía de plantas que habían sido cosechadas una sola vez (al principio del estudio) y que no fueron recosechadas. Los pesos de las coronas obtenidas en la segunda cosecha fueron significativamente menores que los pesos de las coronas obtenidas en la primera cosecha de las mismas plantas dos años antes. El efecto neto de un solo evento de cosechar fue una reducción de casi el 80% del volumen de la porción de las plantas por encima del suelo. Estos datos reflejan lo que está ocurriendo a escala masiva en el hábitat donde el peyote se está cosechando comercialmente. Los números anuales de coronas de peyote que se están cosechando todavía no han disminuido, debido al número creciente de coronas producidas como consecuencia de cosechar. Pero el tamaño promedio de las coronas en el mercado reglamentado del peyote sí ha disminuido notablemente debido al cosechar demasiado temprano las coronas inmaduras de recrecimiento. Estos resultados—con énfasis en la reducción conspicua del tamaño promedio de los individuos—son típicos de poblaciones sobrecosechadas de especies recolectadas de la naturaleza, como por ejemplo el ginseng. La conclusión para la gestión de la conservación es reducir la frecuencia de cosechar el peyote silvestre permitiría que las coronas de recrecimiento maduren con respecto al tamaño—reduciendo así el número de coronas por dosis requerido para el consumo sacramental. También permitiría que las coronas de recrecimiento maduren sexualmente, lo que eliminaría efectivamente la supresión de la producción de semillas para la próxima generación.

INTRODUCTION

Lophophora williamsii (Lem. ex Salm-Dyck) J.M. Coult. (Cactaceae), commonly known as peyote, is a small, spineless, globular cactus native to the Tamaulipan Thornscrub and Chihuahuan Desert of northeastern Mexico and areas close to the Rio Grande in South Texas and Trans-Pecos Texas (Figs. 1a, 2). A literature consisting of hundreds of published works on peyote goes back to early writings shortly after the Spanish conquest of Mexico (e.g., Hernández 1628). The human use of peyote for medicinal (Schultes 1938) and/or religious purposes (Stewart 1987) dates back to at least 6,000 years ago in the Lower Pecos region of the Chihuahuan Desert (Terry et al. 2006). Cultural, botanical, pharmacological, chemical, legal and taxonomic aspects of peyote and its conservation status up to the mid-1990s are summarized by Anderson (1996).

Peyote contains more than 50 alkaloids (Anderson 1996), which impart a bitter taste to the cactus (TH, pers. obs.). That flavor, plus the fact that some of the alkaloids cause physiological effects that could be interpreted as aversive, appear to deter most herbivores from eating the crowns (photosynthetic aerial tops of stems, aka "buttons") of peyote, with the notable exceptions of snails (Fig. 1b) and humans. Of the major alkaloids in *L. williamsii*, the predominant psychoactive compound is a phenethylamine called mescaline, whose effects on human perceptual function were described by Huxley (1954). In the all-night ceremonies of the Native American Church, peyote is ingested by the participants as a psychoactive sacrament, in the form of fresh cactus, dried buttons, or tea. The pharmacological action of the peyote in the central nervous system, potentiated by the auditory stimulation produced by traditional peyote songs accompanied by a water drum and a gourd rattle shaken at a particular frequency, induces a spiritually receptive state which led the Comanche chief Quanah Parker to observe (Simmons 1968): "The white man goes into his church house and talks *about* Jesus, but the Indian goes into his tipi and talks *to* Jesus."

Reports of decline and decimation of natural populations of peyote have intensified over the past two decades (Anderson 1995, 1996; Trout 1999; Terry & Mauseth 2006; Powell et al. 2008; Terry 2008a,b,c). But no national or international government or conservation organization currently lists *L. williamsii* as endangered or even vulnerable – except for the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES), which lists all species of the Cactaceae in Appendix II, which "includes species not necessarily threatened with extinction, but in which trade must be controlled in order to avoid utilization incompatible with their survival" (CITES 1973). It may be argued that *L. williamsii* has a relatively large binational geographic range, and that there exist many healthy populations wherein the species is "common" (W.A. Fitz Maurice, in litt. 2011). However, those who have spent long periods of time in the field observing the well known populations—e.g., those populations reported and collected by Anderson (1960, 1969)—recognize that many of those populations are showing increasing signs of deterioration (decreased size and numbers of individuals, and decreased land area where *L. williamsii* can be found at all), and that the harvesting pressure on these populations appears to be increasing (MT, KT, BW, TH, pers. obs.). It is of interest that the far-sighted Mexican federal regulation NOM-059-SEMARNAT-2010 places *L. williamsii* in the conservation category which denotes that this is a species "subject to special protection" (SEMARNAT 2010). This position of the

Fig. 1a. ***Lophophora williamsii*** **(peyote) in habitat at the study site near the Bordas Escarpment in South Texas. Visible are nine crowns (each crown is the photosynthetic apical portion of a stem or stem branch); one is very small at bottom right. When a crown is removed by cutting it off at ground level with a sharp instrument such as a machete, it becomes a "button" in the commercial peyote trade. Note the dense tangle of woolly trichomes concealing the apical meristems at the center of the largest crowns. The areole on each tubercle of a mature crown bears a tuft of trichomes. The tubercles are arranged in radial rows, and each such row of tubercles marks the midline of a rib. The two largest crowns shown have 13 ribs each. The middle-sized crown at bottom center has eight ribs. The small crown at top center has five ribs. The largest crowns shown are ca. 6–7 cm in diameter.**

Mexican government is particularly significant because over 80% of the land comprising the geographic range of *L. williamsii* is Mexican territory. The most recent and relevant deliberations of the International Union for the Conservation of Nature (IUCN) on updating the conservation status of cacti of the Chihuahuan Desert have not been finalized as of this writing (B. Goettsch, in litt. 2011).

While much of the damage to peyote at the population level has been logically—but anecdotally—attributed to improper harvesting techniques and/or excessively frequent harvesting (TH, pers. obs.), there are no published studies to confirm or refute such claims or to characterize and quantify the effects of harvesting on subsequent production of harvestable peyote in its natural habitat. There is, however, considerable interest in the conservation of peyote among cactus conservationists, including many members of the Native American Church (NAC), whose members use peyote for legally protected religious purposes (TH, pers. obs.). Since anatomical aspects of the regrowth of peyote and best harvesting practices were explicated in a previous study (Terry & Mauseth 2006), the present study focused on the effects of harvesting per se (using best practices) on the survival and regrowth of this species *in situ* in South Texas.

MATERIALS AND METHODS

The study site was located in Jim Hogg County, Texas, within the area designated by Morgan and Stewart (1984) as "commercial peyote range" that extends westward to the Rio Grande from a geologic feature known as the Bordas Escarpment, which runs from Rio Grande City (on the Mexican border in Starr County) north to

Fig. 1b. A solitary peyote cactus near Rio Grande City in Starr County, Texas. Note the damage to the crown inflicted by herbivorous snails. The peyote crown is slightly less than 4 cm in diameter and has eight ribs (the rib on the right is eroded by snail feeding).

an area about 40 miles east of Laredo, Texas. The vegetation of the study site was typical of the Tamaulipan thornscrub that covers much of South Texas and adjacent northern Tamaulipas, Mexico. The study site was chosen because it showed only minimal signs of previous harvesting, and because it was isolated by distance from paved roads, which fact provided some reduction of the risk that the study would be compromised by the activities of peyote poachers.

One hundred peyote plants located along a belt line transect through the population were individually numbered and tagged. Fifty of the individuals were harvested by cutting off the crown at ground level with a carpet knife at the beginning of the study and the other 50 individuals were left unharvested at that time as controls. After two years, the surviving plants in the harvested group (a total of 42 of the original 50 plants) were divided into two subgroups. One of these subgroups (n = 20 plants) was harvested for a second time. The other subgroup (n = 22) was not harvested a second time.

Data on the survivorship of plants and on crown characteristics were collected annually for two years. Crowns are the photosynthetic aerial portions of the cactus stems, which, once cut off from the rest of the plant with a sharp instrument, are referred to as "buttons" in the peyote trade. Crown number and morphology were quantified by counting the number of crowns per plant and the number of ribs per crown, measuring the diameter of each crown, and weighing the harvested crowns in the fresh (not desiccated) state.

From these data, we calculated the total biomass harvested from each plant on each harvest date. For each plant we counted the number of ribs on each crown, summed the rib numbers across all crowns on the plant, and divided the total by the number of crowns on the plant to obtain the mean number of ribs per crown for

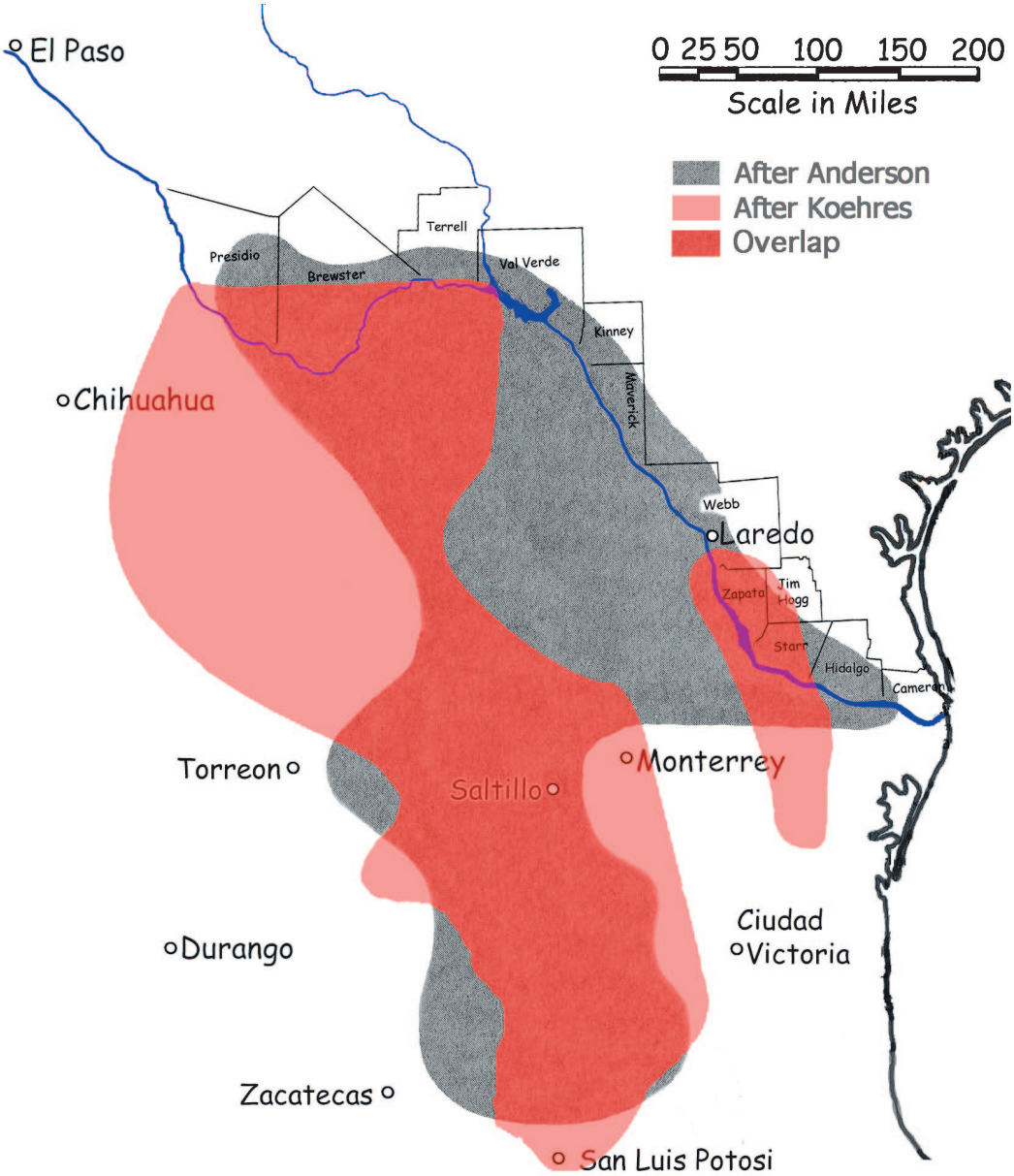

Fig. 2. Geographic distribution of *Lophophora williamsii* (peyote). Note that this is primarily a Mexican species, with over 80% of the land area in its geographic range in Mexican territory. Curiously, in Texas (the only U.S. state where the peyote occurs naturally) the plant is restricted to a narrow strip of land that to a large extent follows the Rio Grande.

that plant. We estimated the volume of each crown as a hemisphere with a radius equal to one-half its measured diameter. (In the case of asymmetrical crowns, whose diameter differed according to the orientation from which the measurement was taken, we measured minimum and maximum diameters [determined by inspection] and took the mean of the two measurements as the "diameter" of the crown in question.) Summing the estimated volumes of all crowns on a given plant gave us an estimate of the above-ground volume of the

plant at each time point in the study. This estimate of above-ground plant volume was linearly related to harvested fresh weight in the first harvest (Fig. 3). Total above-ground volume (hereafter, volume) per plant had the skewed distribution typical of plant sizes (a few large plants, many small plants) and was log-transformed before analysis; this transformation was sufficient to yield normal residuals in an ANOVA. Differences in mass between harvests were normally distributed without transformation. Kruskal-Wallis non-parametric tests were used to analyze the number of crowns per plant and several measures of within-plant morphology: crown diameter, crown volume, ribs/crown, and ribs/volume. Because so few plants died, survival was tested with Fisher's exact test. Of the 90 surviving plants, one was missing data on rib number and therefore does not appear in analyses involving rib number. All statistical analyses were done with SAS 9.1 (SAS Institute, Cary, NC, USA).

RESULTS

Survival.—A higher proportion of control plants than harvested plants survived, but the difference was not significant (97.92% of control plants versus 89.58% of harvested plants; Fisher's exact test, $P = 0.20$).

Plant size.—Two years after harvesting, the unharvested plants had significantly larger total volumes, on average, than the harvested plants did (ANOVA, $N = 90$, $F = 58.31$, $P < 0.0001$; back-transformed means were 22.75 cm^3 and 4.01 cm^3, respectively) (Fig. 4).

This difference in plant size affected the yield of the second harvest. The summed fresh weight of all crowns on a plant in the second harvest was, for 19 out of the 20 re-harvested plants, less than the fresh weight of the originally-harvested single crown of that plant. The average difference in plant mass between the two harvests was 13.98 g (std. dev. = 9.29), which is significantly different from zero ($N = 20$, $t = 6.73$, $P < 0.0001$). Although larger plants had higher yields in both harvests ($r = 0.82$, $P < 0.0001$, $N = 20$), initial plant size did not reduce the negative effects of the initial harvest on the yield of the second harvest: the larger the initial size, the larger the difference in mass between the two harvests (Fig. 5).

Measured fresh weights of crowns obtained in the two harvests were closely related to estimated volumes of the same crowns (first harvest: r_s(volume, mass) = 0.89, $P < 0.0001$; second harvest: $r_s = 0.95$, $P < 0.0001$; $N = 20$; volume was not normally distributed so Spearman non-parametric correlation coefficients are reported here). As one would therefore expect, the change in volume between harvests was strongly correlated with initial volume ($r_s = 0.96$, $P < 0.0001$) and somewhat less strongly correlated with the change in mass ($r_s = 0.67$, $P = 0.0016$).

Plant morphology.—Harvesting altered plant morphology (Table 1; Fig. 6). The initial harvest significantly increased the number of crowns per plant, from a median of one to a median of two per plant (Kruskal-Wallis test, $\chi^2 = 22.29$, df = 1, $P < 0.0001$). However, the crowns on these harvested plants were significantly smaller, with fewer ribs (Kruskal-Wallis test of estimated volumes, $\chi^2 = 56.13$, df = 1, $P < 0.0001$; Kruskal-Wallis test of ribs/crown, $\chi^2 = 37.71$, df = 1, $P < 0.0001$).

Effect of feral hogs.—An unanticipated phenomenon, which added complexity and uncertainty to our interpretation of some of the missing specimens on the transect, was the activity of feral hogs at the study site. Whenever we found a missing peyote specimen, it was necessary to make a determination of the cause of the disappearance of the tagged plant and to classify the presumed death of the plant as harvest-related or non-harvest-related. In some cases we could locate neither the peyote plant nor its tag nor even the metal stake to which the tag had been wired. The use of an appropriate metal detector (Minelab X-Terra 305) eventually resulted in the location of all of the lost plants that had merely been covered by soil washed down the slope by heavy rains. But where there was clear evidence of feral hog rooting, some missing plants were never found. Feral hogs are a non-native species in the region; they began to increase rapidly in population in the area of the study site in the early 1990's (C.W. Hellen, pers. comm.). Accordingly, we decided to exclude from the study those plants which we determined to be missing as a result of feral hog activity. Fortunately there were only two hog-implicated missing plants excluded from the harvested group of 50 plants, and an equal number of such plants were excluded from the control group. It should be noted that if we had counted these missing

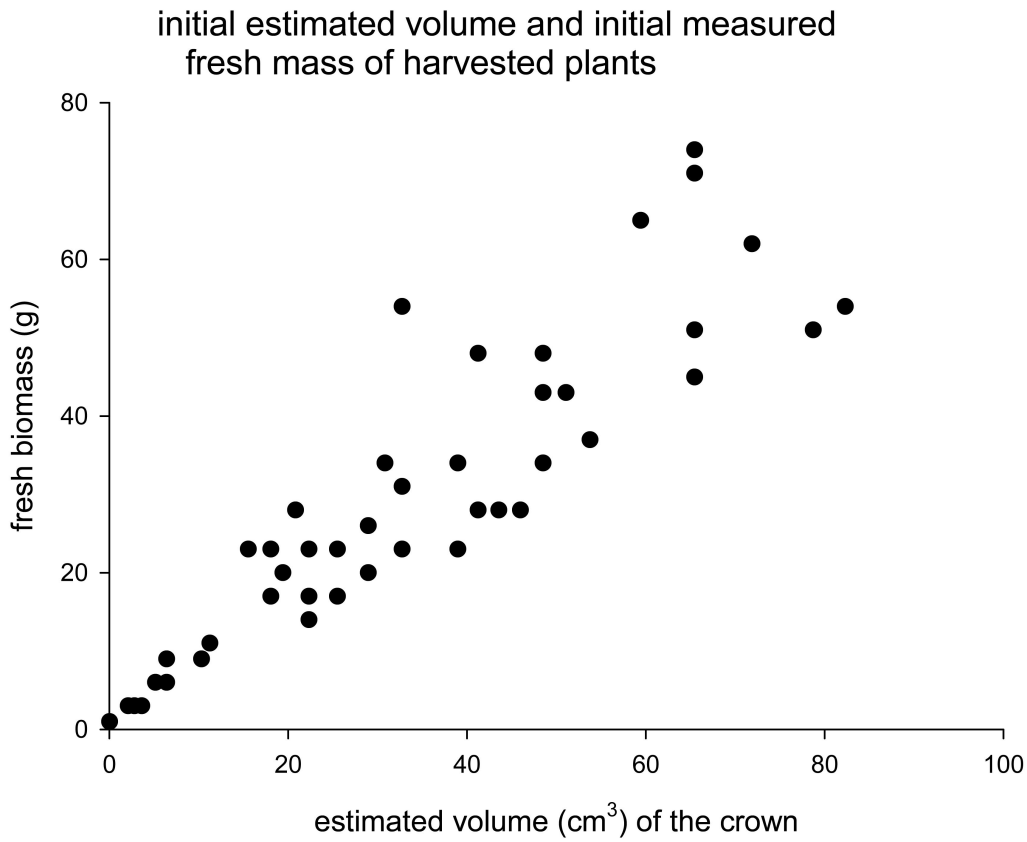

Fig. 3. Initial estimated volume and initial measured fresh weight of crowns harvested at beginning of study. Volume of each crown was estimated as a hemisphere with radius equal to half the measured diameter of the crown. Estimated volume and fresh weight are closely related (Spearman non-parametric correlation coefficient $r_s = 0.91$). This fact is useful because there were no detached crowns to be weighed in the control group of unharvested plants, which meant that the only way to compare the sizes of harvested crowns and those of unharvested crowns was by their volumes, based on diameter measurements.

plants as harvest-related deaths instead of excluding them from the study, that interpretation would have tripled the mortality in the control group from ca. 2% to 6% and increased the mortality in the harvested group from ca. 10% to 14%.

DISCUSSION

The observed increase in the number of crowns (i.e., buttons) per plant that resulted from the initial harvest is compatible with the common belief that "…harvesting [is] conducive for Peyote growth, and…harvesting also increases the number of new plants" (Morgan 1976). Harvesting may not affect survival, as the observed arithmetic reduction in survival was not significant. However, harvesting clearly reduced crown size so much that the negative effect of harvesting on crown size outweighed the increase in crown number also caused by harvesting. A parallel decrease in the fresh weight of the crowns of plants that were reharvested after two years, was also observed. This empirical result of harvesting—somewhat larger numbers of substantially smaller peyote buttons—suggests that our experimental protocol adequately modeled the system of commercial harvesting that generates the peyote buttons being offered for sale by licensed peyote distributors in South Texas, which has resulted in mostly very small, immature buttons being offered for sale (as seen in Fig. 7).

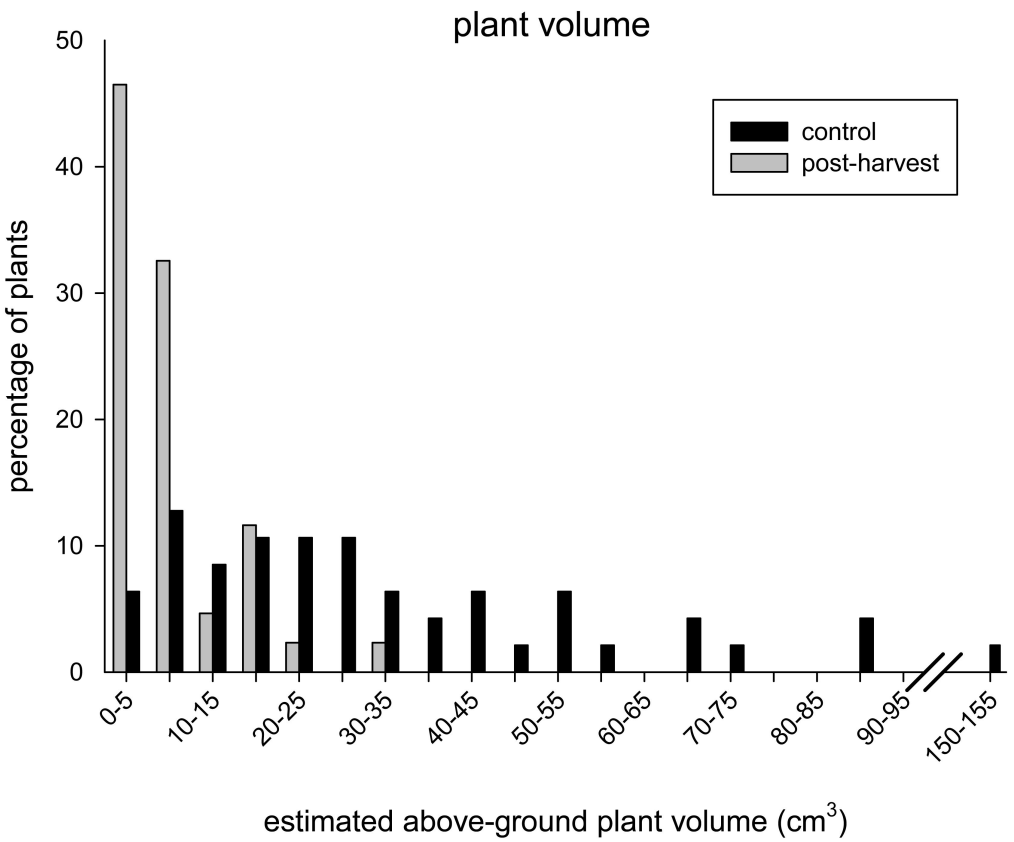

Fig. 4. Distribution of above-ground plant volumes (summed crown volumes for each plant, estimated as in Fig. 1), two years after initial harvest. Note the high frequencies of the smallest plant size categories in the harvested group (gray bars), and the moderate to low frequencies of a wide range of different sizes of plants in the control group (black bars). The largest sizes of plants in the control group were not observed at all in the harvested group. The harvested group had many more small plants than did the control group. This comparison of plant volume frequency distributions is one way of portraying the marked reduction in above-ground plant size that results from harvesting.

Annual peyote sales data covering the last quarter century are presented in Figure 8. One curve, showing the total annual sales of peyote in dollars, has an overall positive slope that is characteristic of many commodities that are subject to ordinary price inflation. The other curve showing total number of buttons sold annually—which we interpret to be a close approximation of the number of buttons harvested annually—indicates that the annual number of buttons harvested is considerably more stochastic, with a substantial downturn from 1986 to 1989, followed by a remarkable rebound from 1990 to the peak of about 2.3 million buttons sold in 1997, and from that point forward, a roughly continuous decrease from 1997 to 2010. Considering only the recent interval from 1997 to 2010, however, the picture is simpler: The positively sloped curve showing total sales in dollars intersects the negatively sloped curve showing numbers of buttons sold (harvested). That is to say, prices have gone up as numbers of buttons sold have gone down, which is rational market behavior when a commodity becomes progressively less available.

The data in Fig. 8 include only the regulated sales by the licensed peyote distributors to documented members of the NAC for legally protected religious use. What percentage of the total market this regulated segment comprises, is an open question. There is minimal hard evidence of smuggling of peyote from Mexico into the U.S. (Gee 1998), but there is clear and abundant evidence that Mexican peyote populations are being

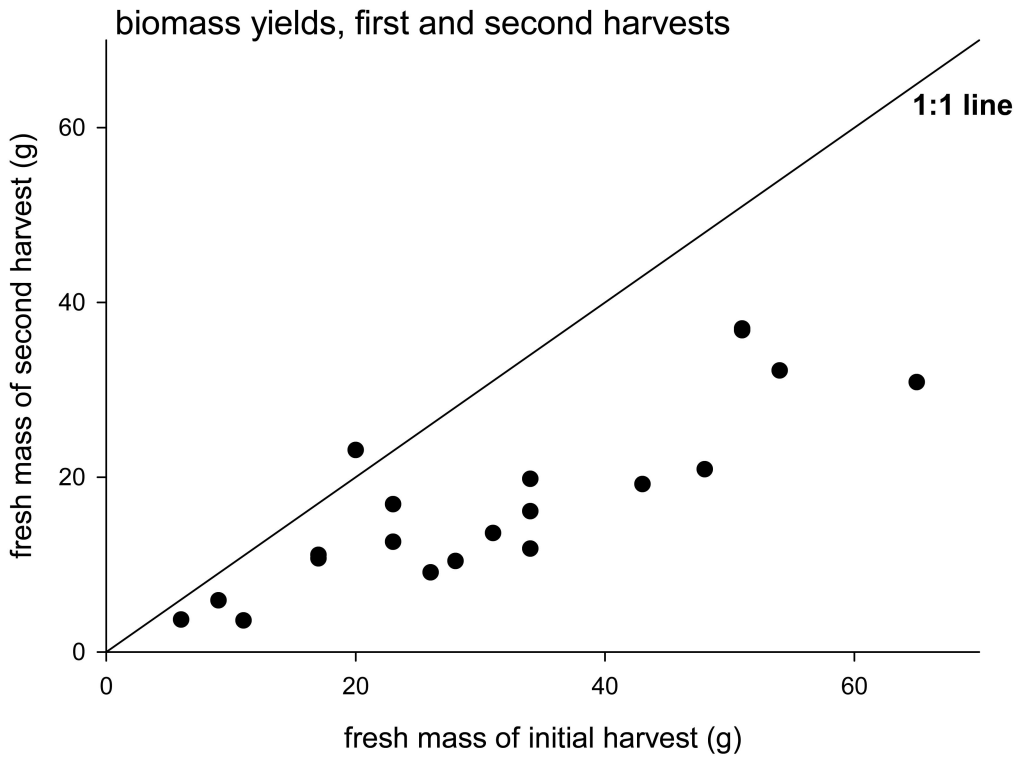

Fig. 5. Biomass yields of first and second harvests from the same individual plants. Fresh weights of harvested crowns of plants that were harvested at the beginning of the study, with the exception of a single data point, were consistently and significantly higher than the fresh weights of regrowth crowns obtained when the same plants were reharvested (i.e., all regrowth crowns were removed) two years later. Such decreasing yield associated with harvesting is a hallmark of an unsustainable system of production.

pillaged by poachers who dig up the entire plants in massive quantities for some unidentified market that requires specifically *L. williamsii* and not the other, non-mescaline-containing species of *Lophophora* that occur in Mexico (Terry 2008a,b,c). No one knows how much peyote is harvested annually by Native Americans who make private agreements with landowners who have peyote growing naturally on their land. And no one knows how much peyote is harvested illegally by poachers who supply the Native American Church or other consumers. We could estimate the annual consumption of peyote buttons in the U.S. by making some assumptions about the number of NAC members in the U.S., the number of peyote meetings attended per NAC member per year, and the average number of peyote buttons consumed per person per meeting. But apparently no one even knows how many members of the NAC there are, due to the fact that the NAC is not a single entity, but rather a totally decentralized set of independent NAC organizations, most of which communicate with each other only sporadically, if at all. The Native American Church of North America (NACNA) is an umbrella organization that represents a relatively small number of relatively large tribal church groups, but it almost certainly represents only a minority of the total membership of all NAC groups in the U.S. Such factual deficiencies notwithstanding, for the sake of a hypothetical calculation let us use an estimate of Anderson (1996) that the total NAC membership is about 250,000. If we divide the current annual regulated sales number of ca. 1.5 million buttons by 250,000 members, we get an average of six peyote buttons per person per year. That might be enough peyote for each member to attend one peyote ceremony per year, if we were talking about full-size mature peyote buttons. But in fact we are talking about small regrowth buttons that constitute most of the offerings in the current regulated peyote market, which means that six buttons per person would not even

Table 1. Average values of selected variables two years after the initial harvest. Standard deviations in parentheses. Study began with 50 plants being harvested and 50 left as unharvested control plants. Plant volume is the sum of the volumes of all the crowns on a given plant; i.e., it is the total volume of above-ground photosynthetic stem tissue, which is identical to the total volume of harvestable "button" tissue that constitutes the commercial product in the peyote trade. No. of crowns/plant was determined by counting. Crown diameter was measured with a ruler scored in mm. Crown volume was calculated as half the volume of a hemisphere having the radius equal to half the measured diameter. Volume so calculated for the crowns of peyote in this study was strongly correlated with weight (Fig. 3). No. of ribs/crown was obtained by counting. (See Figs. 1a, 1b for depiction of ribs and examples of rib numbers.)

Variable	Control plants	Harvested plants
Plant volume[1]	32.46 cm^3 (28.48)	6.94 cm^3 (6.66)
No. of crowns/plant	1.70 (1.56)	2.60 (1.13)
Crown diameter[2]	40.10 mm (11.96)	19.39 mm (6.04)
Crown volume[2]	22.17 cm^3 (16.67)	2.77 cm^3 (2.46)
No. of ribs/crown[2]	9.30 (2.35)	6.79 (0.77)

[1]Estimated from crown diameter for each crown separately, then summed.
[2]These are means of means: averaged across all crowns on a plant, then averaged across all plants.

suffice for an adequate dose of sacrament for every member to participate in one ceremony per year. We know that one meeting per year is nowhere near the cultural norm for the frequency of meetings in the NAC. Some churches may hold meetings almost weekly—say, 50 meetings per year (Bobby Pedro, pers. comm.). If all NAC groups held meetings at such a frequency, then more than 50 times the amount of peyote sold in the regulated system would be required to meet the needs of the NAC for sacrament. Even with a lower frequency of meetings and assuming that not all NAC members attend meetings every year, the daunting magnitude of the disparity between the amount of peyote sold and accounted for in the regulated peyote trade and the amount likely to be required by the NAC seriously erodes the credibility of the proposition that most of the peyote supplied to the NAC comes through regulated channels.

Why have the annual numbers of buttons sold not decreased more drastically and consistently to reflect the damage being done to the wild peyote populations? And why does the market price of peyote appear not to have risen more sharply as well? The high frequency of harvesting, modeled by a two-year interval between harvests in the present study, together with the related decrease in the size of regrowth buttons, provides plausible answers to those questions. Our results suggest that the numbers of buttons sold annually have not decreased as dramatically as one might expect because the harvesting of solitary mature crowns increases the number of buttons in a population by stimulating lateral branching from areoles on the subterranean portion of the stem of a decapitated plant, which often results in the regrowth of multiple, but much smaller, crowns per plant.

The effect of harvesting on price to the consumer (as opposed to total gross sales revenue to the vendors) is more dramatic than the data of Fig. 8 suggest, because Fig. 8 does not take into account declining button size. A few decades ago the harvesting frequency of peyote was lower, and the buttons being harvested for sale to the NAC were principally mature crowns similar to the larger plants in the present study (Mauro Morales, pers. comm.). Now, however, the harvesting frequency has generally increased and mature plants are relatively scarce (Morales, pers. comm.), with the result that the market is dominated by small regrowth crowns similar to those in the harvested group in the present study. In terms of weight, whereas commercial peyote a few decades ago would have typically consisted of buttons weighing on the order of 25–30 g each on average (Morales, pers. comm.), now the average weight of a button, like the average weight of the individual second-harvest crowns in the twice-harvested group in this study (5.8 g), is likely to be in the single-digit range in grams. The price increased from $78/1000 buttons to $310/1000 buttons from 1986 to 2010, a fourfold nominal increase, but only twofold after adjusting for inflation (Bureau of Labor Statistics http://www.bls.gov/data/inflation_calculator.htm). If, however, buttons were only one-fifth as large in 2010, the price per gram was actually ten times higher in 2010 than in 1986. Increasing unit prices, like declining harvests (Fig. 6) and declining individual size (Fig. 2), are a common consequence of unsustainably high rates of harvest (Allen et al. 2005).

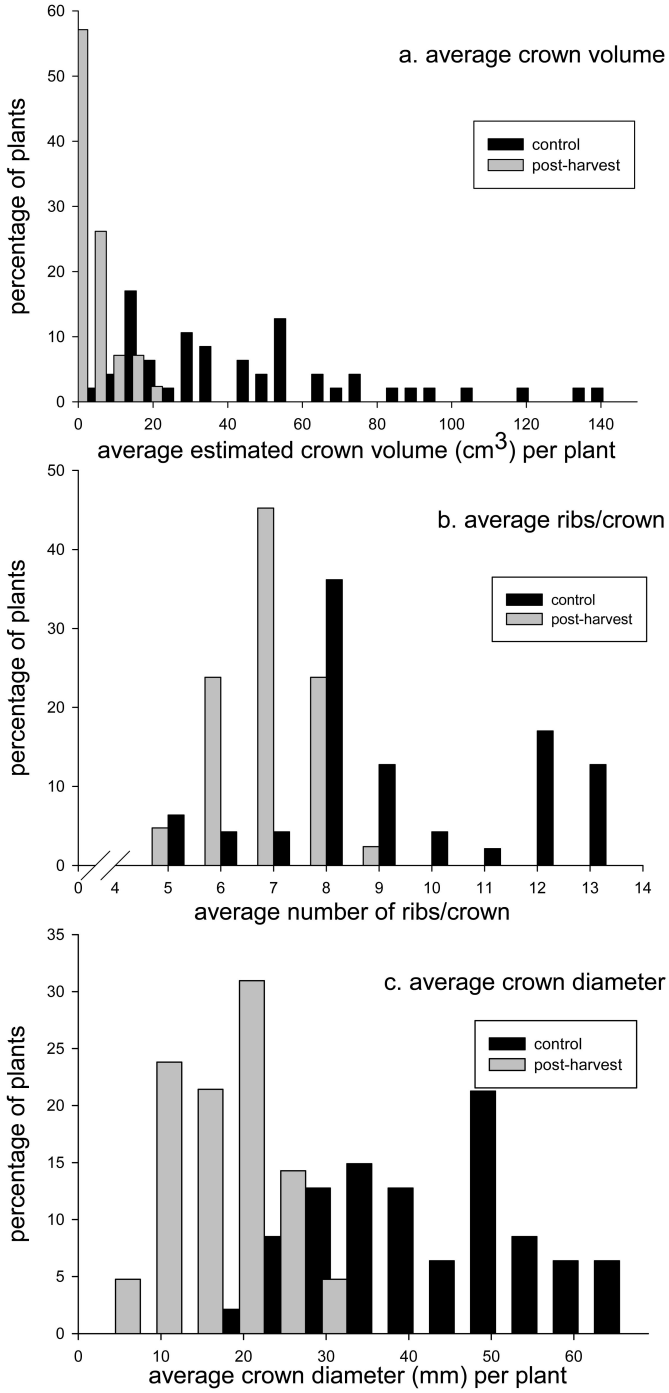

FIG. 6a. Distribution of average crown volume per plant. The average crown volume was calculated for each plant. Average crown volume for a given plant is the summed crown volume of Fig. 4 divided by the number of crowns on the plant. For the many control plants that had only one crown, average crown volume is equal to average plant volume of Fig 4. For harvested plants, which often had more than one crown, average crown volume is a fraction of average plant volume. For those harvested plants that showed no regrowth, the average crown volume is zero. Note that the majority of harvested plants show average crown volumes in the smallest size bin (≤ 5 cm^3), and ca. 85% of the harvested plants show average crown volumes in the two smallest size bins (≤ 10 cm^3). In contrast, the control plants have average crown volumes in 20 different size bins across the entire range of average crown volumes from 0 to 140 cm^3. This is another way of portraying the reduction in average crown size associated with harvesting.

FIG. 6b. Distribution of average number of ribs per crown, per plant. For plants with only one crown, this is equivalent to the number of ribs per plant. Otherwise, it represents an average of all crowns on a plant. Rib number is roughly correlated with size and age of the crown. Note the modal values of 8 ribs for control plants and 7 ribs for harvested plants. Eight is the Fibonacci number of ribs characteristic of a crown of a young adult plant; most control plants in this study had only one crown, of 8 ribs. The modal value of 7 ribs/crown in harvested plants reflects the presence of immature as well as mature crowns on these plants. The Fibonacci number 13 is the maximum rib number observed for the control plants, as it is for the species. The minimum rib number observed in both harvested and control plants is the Fibonacci number 5, as is likewise true of the species.

FIG. 6c. Distribution of average crown diameter per plant. Crown diameters are not as dramatically different between control and harvested plants as are estimated volumes (Fig. 4), because volume is a function of the cube of the radius (i.e., the cube of half the diameter). Nevertheless, note the relatively small area of overlap in the values of this variable for harvested vs. control plants. This is yet another way of depicting that the regrowth crowns of harvested plants are generally smaller than the crowns of nonharvested control plants.

Fig. 7. Small peyote buttons in a drying bin at a licensed peyote distributor's place of business in South Texas. Most of the buttons shown are less than 4 cm in diameter, and many are less than half that size (Photo by Kurt Böhme).

It is tempting to carry the argument one step farther and hypothesize that the concentration of mescaline (the predominant and most potent psychoactive alkaloid in peyote) in the regrowth buttons is likely to be considerably lower than that in the crowns of mature plants not previously harvested. That notion is compatible with anecdotal complaints by NAC members about the "sweet" taste (suggesting low levels of the alkaloids that normally impart a bitter taste to peyote) and low psychoactive efficacy of the small buttons currently being sold in the trade (TH, pers. obs.). If true, such a deficiency in mescaline concentration associated with the immaturity of the small regrowth buttons would be adding an additional hidden component to the real per-gram price of peyote associated with excessively frequent harvesting, as a greater quantity of tissue from immature crowns would be required to provide the same dose of mescaline as would be obtained from the "normal" (smaller) quantity of tissue from mature plants. The analytical chemistry work comparing the mescaline concentrations of mature first-growth crowns and immature regrowth crowns is currently in progress (Terry et al., in preparation), but the data are not yet available.

Another notable result was the significant decrease in the biomass (measured as fresh weight) of the second harvest, compared to the biomass yielded from the same individual plants in the initial harvest two years previously at the start of the study. It is reasonable to infer from this decreased second-harvest yield that the time interval of two years between harvests is too short to be sustainable. Yet judging from the size of the peyote buttons currently being offered for sale in the trade, two years appears to be a commonly accepted period of time to allow regrowth prior to the next harvest (MT, pers. obs.). Similar decreases in individual size have occurred in other wild-harvested species, where they often indicate unsustainable levels of harvesting (e.g., Hall

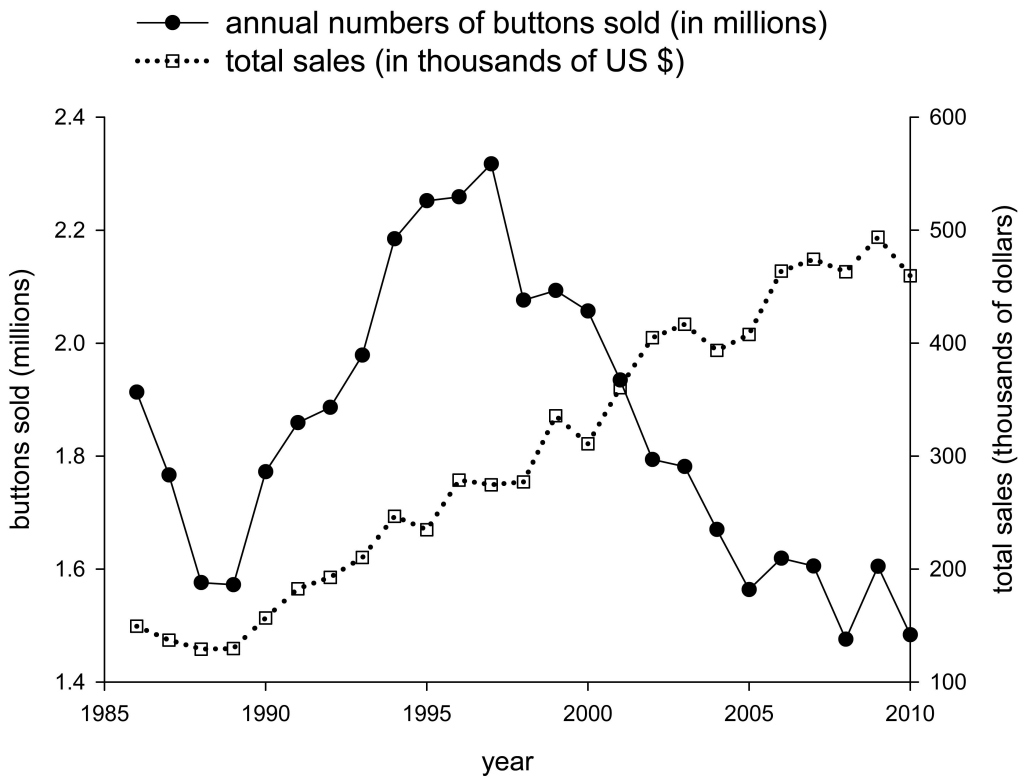

Fig. 8. Annual sales of peyote by licensed distributors, 1986–2010. Solid curve: numbers of buttons sold (in millions—see vertical axis at left). Dotted curve: total sales (in thousands of dollars—see vertical axis at right) paid for the annual crop by NAC members. The marked decrease in the average size of buttons that has occurred over recent decades is not shown and is not inferable directly from these data. Drawn from data obtained from Texas Department of Public Safety in 2011.

and Bawa 1993; Nantel et al. 1996; McGraw 2001; Berkeley et al. 2004; Case et al., 2007; Genner et al. 2010). The literature on overharvesting of ginseng (*Panax quinquefolia*) is particularly relevant to our findings on peyote. Genner et al. (2010) determined from herbarium specimen collection data that there has been a long-term decrease in the overall population size (number of individuals counted in a systematic census) of ginseng as a species in specific regions of its geographic range. Case et al. (2007) showed from herbarium specimen data that the size of individual ginseng plants collected has decreased over a period of decades. Nantel et al. (1996) used mathematical modeling and population data to show that both harvesting frequency and harvesting intensity (defined as the percentage of individuals harvested from a population each time the population is harvested) are key factors in reducing the population growth rate of ginseng. For example, given a harvesting frequency of once every five years, harvesting 30% of the individuals in a population at each harvesting event would be sufficient to reduce the population growth rate below the equilibrium value of 1.0, where the death rate due to harvesting is exactly equal to the reproductive replacement rate of individuals. When the growth rate falls below the equilibrium value, population size decreases, and a decrease in population size is the ultimate criterion for unsustainable harvesting. The decrease may be postponed and temporarily masked in the case of peyote by an initial post-harvest proliferation of small regrowth crowns that elevate the census despite the reduction in total population biomass. Another reliable indicator of unsustainable harvest is a decrease in the average size of harvested individuals, as found by Case et al. (2007) with ginseng and in the present study with peyote. It should be noted that, in terms of the Nantel et al. (1996) model, the harvesting intensity in the

harvested group of peyote plants in the present study was 100%; i.e., all plants in that group were harvested. This fact, and the fact that regrowth of the harvested commodity occurs in peyote, constitute important differences between peyote and ginseng. With wild ginseng, harvesting intensities may be lower than for peyote, but every ginseng plant that is harvested is a plant removed from the population—that is, a death, insofar as the population is concerned. That is not true of peyote, which has the ability to produce regrowth from the subterranean stem, if the latter survives the harvesting process.

One additional observation from our experience suggests that for long-duration plant studies conducted *in situ* in South Texas, it may be worth considering building a sturdy exclosure fence around the study site before starting the study, to exclude feral hogs.

Conclusions as to optimizing the management of natural peyote production must be considered preliminary at this point, as this report covers only the first two years following a controlled harvesting event in a peyote population that had minimal signs of previous harvesting. It is quite conceivable that delayed differences in survivorship attributable to the initial harvest may be discernible by the four-year time point in this ongoing study. At that time there will also be survivorship data associated with the second harvest, as well as data on the biomass yield from a third harvest for comparison with the first two harvests reported here. What we can state now with confidence, based on the data presented here, is that (1) a two-year interval between peyote harvests is too short to be sustainable, and that, (2) in light of the reduced total biomass yield of the second harvest compared to the first, the economically adverse effect of harvesting on button size outweighs the beneficial effect of harvesting on number of buttons per plant.

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