LIMITATIONS TO NATURAL PRODUCTION OF *LOPHOPHORA WILLIAMSII* (CACTACEAE) II. EFFECTS OF REPEATED HARVESTING AT TWO-YEAR INTERVALS IN A SOUTH TEXAS POPULATION

Martin Terry

Sul Ross State University
Department of Biology
Alpine, Texas 79832, U.S.A.
mterry@sulross.edu

Keeper Trout

Cactus Conservation Institute
P.O. Box 561
Alpine, Texas 79831, U.S.A.

Bennie Williams

Cactus Conservation Institute
P.O. Box 561
Alpine, Texas 79831, U.S.A.

Teodoso Herrera

Rio Grande Native American Church
P.O. Box 460346
San Antonio, Texas 78246, U.S.A.

Norma Fowler

The University of Texas at Austin
Department of Integrative Biology C0930
1 University Station
Austin, Texas 78712, U.S.A.

ABSTRACT

In 2008 we began a long-term study of the effects of harvesting on a wild population of the cactus *Lophophora williamsii* (peyote), including harvesting treatments similar to those used to harvest it for legally protected religious use by members of the Native American Church. Here we assess the effects of harvesting in three different treatments: (1) plants that were harvested once, (2) plants that were harvested every two years (typical of commercial harvesting rates), and (3) control plants that were never harvested. After four years, the survival rate was significantly greater in the unharvested control plants (94%) than in the harvested plants (73%). Average harvested mass of fresh tissue per plant decreased significantly (by 44%) between the first and second harvests, and then further decreased significantly (by 32%) between the second and third harvests. The average number of crowns per plant, which increased after the first harvest, decreased after the second harvest. Estimated total volume of the above-ground crown(s) of each plant, which was closely related to harvested plant mass, was used to compare growth rates between treatments. The average growth rate of the multiple-harvest plants was significantly lower than the average growth rates of plants in the other two treatments. Growth rates in the control and single-harvest treatments did not differ significantly in 2012, but because the single-harvest plants were so much smaller than the control plants in 2010, they remained smaller than the control plants in 2012. The annual number of crowns harvested and sold commercially as “buttons” by licensed peyote distributors continued its slow decrease in 2011, while the price per unit continued to rise. These trends and the results of this study all indicate that present rates of peyote harvest are unsustainable.

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

RESUMEN

En el año 2008 empezamos un estudio a largo plazo sobre los efectos de cosechar el cactus *Lophophora williamsii* (peyote) en una población silvestre, utilizando tratamientos de cosechar similares a los que se utilizan para cosechar el peyote para su legalmente protegido uso religioso por los miembros de la Native American Church. Aquí evaluamos los efectos de cosechar en plantas de tres tratamientos distintos: (1) plantas que se cosecharon una sola vez, (2) plantas que se cosecharon cada dos años (cual tasa es típica en la cosecha comercial), y (3) plantas controles que no se cosecharon nunca. Después de cuatro años, la tasa de supervivencia fue significativamente mayor en las plantas controles (94%) que en las plantas cosechadas (73%). En el promedio la masa de tejido fresco cosechado disminuó significativamente (por un 44%) entre la primera cosecha y la segunda, y después volvió a disminuir significativamente (por un 32%) entre la segunda cosecha y la tercera. El número mediano de coronas por planta, lo cual se aumentó después de la primera cosecha, disminuó después de la segunda cosecha. El volumen total aproximado de las coronas por encima del suelo de cada planta, lo cual fue muy cercamente relacionado al peso del tejido cosechado de la planta, se utilizó para comparar las tasas de crecimiento entre los tratamientos. La tasa de crecimiento mediana de las plantas cosechadas más de una vez fue significativamente más baja que las tasas de crecimiento medianas de las plantas en los otros dos tratamientos. Las tasas de crecimiento en el tratamiento control y el tratamiento de una sola cosechada no fueron significativamente diferentes en 2012, pero por el hecho de que las plantas de una sola cosechada fueron mucho más pequeñas que las plantas controles en 2010, todavía se quedaron más pequeñas que las plantas controles en 2012. El número anual de coronas cosechadas y vendidas comercialmente como “botones” por los distribuidores registrados de peyote siguió disminuyendo en 2011, mientras que el precio por unidad siguió subiendo. Estas tendencias y los resultados de este estudio todos indican que las tasas actuales de cosechar el peyote no son sostenibles.

J. Bot. Res. Inst. Texas 6(2): 567 – 577. 2012

INTRODUCTION

Lophophora williamsii (Lem. ex Salm-Dyck) J.M. Coult. (Cactaceae), known as peyote both in Spanish and in English, is a small cactus (rarely exceeding 10 cm in diameter) of northeastern Mexico and adjacent border areas of Texas. The aerial crowns of plants are approximately hemispherical in shape. Some plants are caespitose; i.e., they have multiple crowns arising from a single rootstock. The literature on the biology of this plant up to the mid-1990s is summarized by Anderson (1996), who first suggested that the species might be endangered by overharvesting (Anderson 1995).

There is active commercial trade in the harvested crowns of peyote, which are collected and sold by licensed distributors to the Native American Church (NAC) for religious use as protected by U.S. law. There is substantial concern that the rate of harvest of peyote from wild populations is not sustainable. Anecdotal reports by members of the NAC include descriptions of the decline or decimation of natural populations and a decrease in both the availability and the quality of peyote being offered for sale in the regulated peyote market (TH, pers. obs.). A number of papers in the scientific literature have described the decline of peyote in its native habitat, apparently due to overharvesting (Anderson 1995; Trout 1999; Terry & Mauseth 2006; Powell et al. 2008; Terry 2008a,b,c; Terry et al. 2011). Despite such reports involving both Texas and Mexican populations, the species is not (yet) considered in danger of extinction (NatureServe 2012; Fitz Maurice and Fitz Maurice 2009), except in Texas, where NatureServe determined it to be in the S4 (imperiled) category. The work of Terry et al. (2011) was the first experimental investigation of the effects of harvesting on peyote plants in situ. In that paper we reported the effects that were detectable two years after the initial harvest. The present report focuses on effects detectable four years after the initial harvest.

MATERIALS AND METHODS

The study site was described in Terry et al. (2011). Because of the multi-year duration of the ongoing study and the complexity of the study design, it is appropriate to provide a clear, detailed description of what was done to which plants, and when.

At the start of the study, in March 2008, 100 *L. williamsii* plants that appeared not to have been previously harvested were individually numbered and tagged along a transect through the population. The number of crowns on each plant was counted and the horizontal diameter of each crown was measured. Fifty of these plants that were single-crowned were then harvested (i.e., the crown of each plant was cut off transversely at ground level and removed), and the other 50 plants (most but not all of which were single-crowned) were left unharvested as controls. The harvested crown of each plant in the harvested group was weighed, to determine the harvested fresh biomass obtained from each of these "virgin" plants.

At the end of the second year of the study, in March 2010, all surviving plants from the original groups of 50 harvested and 50 control plants were located, the number of crowns on each plant was counted, and the diameter of each crown was measured. Then the 43 surviving plants in the harvested group were divided into two subgroups: 20 multiple-harvest plants and 23 single-harvest plants. All regrowth crowns were harvested from the 20 multiple-harvest plants, leaving these now twice-harvested plants without crowns (and thus without photosynthetic tissue) for the second time in two years. Reharvest at two-year intervals is typical in current commercial harvest (MT, pers. obs.). The harvested crown(s) of each multiple-harvest plant were weighed to obtain harvested fresh biomass at a second harvest. A comparison of harvested biomass between the 2008 and 2010 harvests was reported by Terry et al. (2011). The single-harvest plants were not reharvested, and the surviving plants of the 50 original control plants continued to serve as unharvested controls.

At the end of the fourth year of the study, in March 2012, all surviving plants were again located, counted, and measured. In addition, all new regrowth crowns were again harvested and weighed from the 16 surviving plants in the multiple-harvest treatment. In summary, control plants have never been harvested, single-harvest plants were harvested once, in 2008, and multiple-harvest plants have so far been harvested three times, in 2008, 2010, and 2012.

All statistical analyses were done with SAS 9.1 (SAS Institute, Cary, NC, USA).

RESULTS

Survival.—Of the 100 plants of the initial (2008) census, 4 (2 control, 2 harvested) were dug up by feral hogs and were therefore dropped from all further analyses, leaving 96 plants. Of these 96 plants, 6 (1 control, 5 harvested) died before the second (2010) census. Ninety plants were still alive in 2010 (census 2): 47 control plants and 43 plants that had been harvested in 2008. Of these 43 surviving plants that had experienced one harvest, 23 were assigned to the single-harvest treatment and 20 were assigned to the multiple-harvest treatment.

Of the 47 control plants alive in 2010, 45 were still alive at census 3 in 2012. Nineteen of the 23 single-harvest plants (83%) and 16 of the 20 multiple-harvest plants (80%) were still alive in 2012. By 2012 the survival rate of control plants from census 1 through census 3 was significantly higher than the survival rate of harvested plants over the same interval (94% [45/48] versus 73% [35/48], $\chi^2 = 8.65$, $P = .0033$; Fig. 1).

Harvested mass.—Weights of all the crowns of a plant were summed to calculate harvested fresh mass per plant. Mass per crown was calculated for each plant by dividing its total mass by its crown number; these values were then averaged for statistical analysis and for Figure 2. Average harvested mass per plant decreased from census to census: 44% between the first and second censuses and 32% between the second and third censuses (Fig. 2, solid line). The differences between harvests were significantly different from zero (paired *t*-tests: harvest 1 vs harvest 2: 14.0 g average difference, N = 20, $t = 6.73$, $P < 0.0001$; harvest 2 vs harvest 3: 6.9 g average difference, N = 16, $t = 4.24$, $P = 0.0007$).

Plants initially responded to harvesting by increasing the average number of crowns per plant (Fig. 2, dashed line), although this increase was not sufficient to counterbalance the decrease in mass per crown (Fig.2, dashed and dotted line). After the second harvest, both the average number of crowns per plant and the average mass per crown decreased.

Volume.—The above-ground volume of each plant was estimated by first estimating the volume of each crown as a hemisphere from its measured diameter: estimated volume = $\frac{2}{3} \pi (\text{diameter}/2)^3$.

The estimated volumes of all the crowns on the plant were then summed to estimate total plant above-ground volume. The estimated volume of each plant in 2012 was very closely correlated with its harvested fresh mass in 2012 (Fig. 3).

Volumes were log-transformed before analysis of covariance (ANCOVA) to improve normality of the residuals. Volume at census 2 (2010) was used as a covariate. Treatments did not differ significantly in their slopes: the slope of the relationship between log-transformed volume in 2010 (x-axis) and log-transformed volume in 2012 (y-axis) was the same for each treatment. Therefore the final ANCOVA model assumed equal slopes. Note that equality of slopes in a model fitted to log-transformed data does not imply that slopes will be linear when untransformed data are graphed on a linear scale (e.g., Fig. 4).

Estimated plant volume at census 3 (2012) was closely related to estimated plant volume at census 2; 74% of the variation in the former was explained by variation in the latter amount. Treatment accounted for an additional 10% of the variation among plants at census 3. The effects of the single-harvest treatment did not differ from those of the control (Scheffé contrast, $F_{1,75} = 1.33$, $P = 0.25$), but each of these treatments differed significantly from the multiple-harvest treatment (Scheffé contrasts; control versus multiple-harvest: $F_{1,75} = 29.20$, $P < 0.0001$; single-harvest versus multiple-harvest, $F_{1,75} = 41.46$, $P < 0.0001$; Fig. 4). In other words, the surviving single-harvest plants were growing (on a logarithmic scale) about as fast as the surviving control plants between 2010 and 2012, but they began the interval with much smaller sizes than the control plants. In contrast, the multiple-harvest plants were decreasing in size. For example, the final ANCOVA model predicts that a control plant with a volume of 10.0 cm^3, the average size of all 90 surviving plants at census 2, would have grown to 21.9 cm^3 and a single-harvest plant of the same size would have grown to 26.3 cm^3 (not significantly different from 21.9 cm^3), but a multiple-harvest plant with a volume of 10.0 cm^3 would have decreased slightly in size, to 9.66 cm^3.

Regional harvesting trends in South Texas.—Annual peyote sales data covering the years 1986–2011 (Texas Department of Public Safety, unpublished data) are presented in Figure 5. Although these figures do not in-

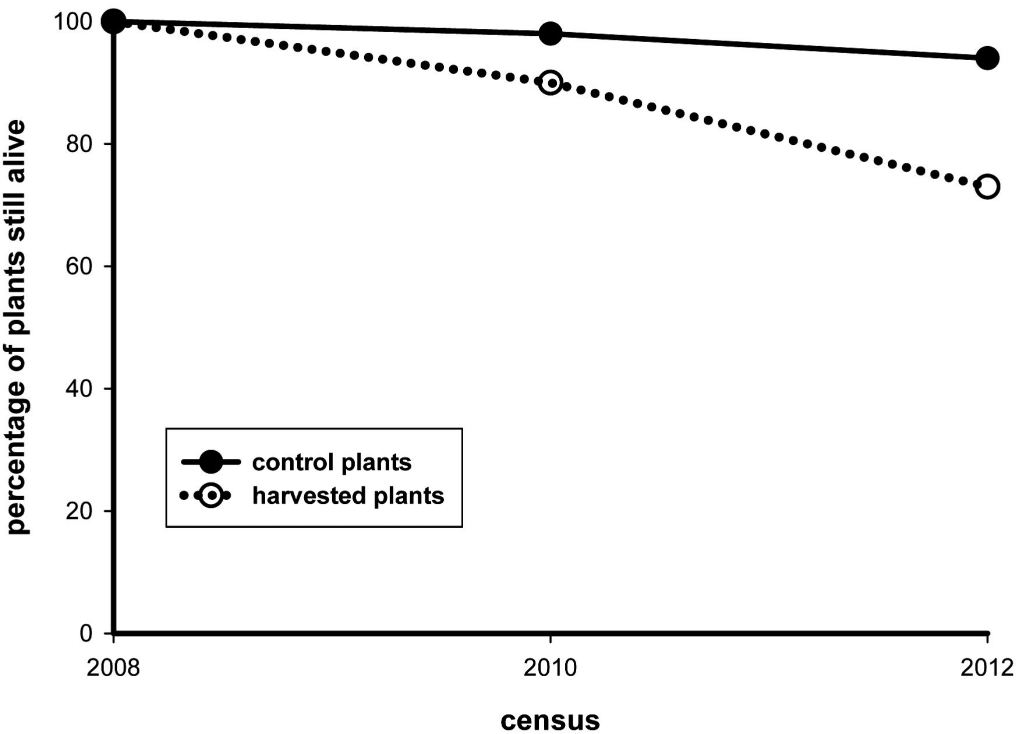

FIG. 1. Numbers of surviving plants at each census. Solid line: control plants; dotted line: harvested plants.

clude all sales of peyote (Terry et al. 2011), it is reasonable to assume that the number of buttons sold in the regulated trade is positively correlated with the total number of buttons harvested in the region of South Texas known as "the Peyote Gardens." In 2011, the DPS-regulated peyote sales totaled slightly over 1.4 million buttons, continuing the generally downward trend which such sales have followed since 1997. It is noteworthy that prior to the current decline there was a decrease in numbers of buttons sold during the late 1980s that appears to have corresponded to the historical decline in the available harvest of mature plants, followed in the early to mid-1990s by a marked increase in numbers of buttons sold when the proliferation of small regrowth buttons began to be harvested to meet the needs of the NAC. Anecdotal accounts from NAC meetings during the period of temporary increase in numbers of buttons noted the prevalence of fresh buttons as small as dimes (TH & KT, pers. obs.). The number of buttons sold in 2011 was the lowest for any year in the last quarter of a century. As the annual number of buttons sold has declined steadily since 1997, the price has shown a marked increase; the price per button is roughly equal to total sales (in U.S. dollars) divided by the number of buttons sold.

DISCUSSION

Effects of harvesting on plant survival and growth

The negative effects of harvesting on survival may be delayed. The initial harvest did not significantly reduce survival during the first two years after the harvest (2008 to 2010; Terry et al. 2011), but its effects were highly significant by 2012 (73% survival to the four-year time point in 2012 among plants harvested in 2008, versus 94% among control plants). Any delayed effects of the second (2010) harvest on survival were not yet evident in 2012.

The effects of precipitation may also be delayed. The six months preceding the 2010 census received sub-

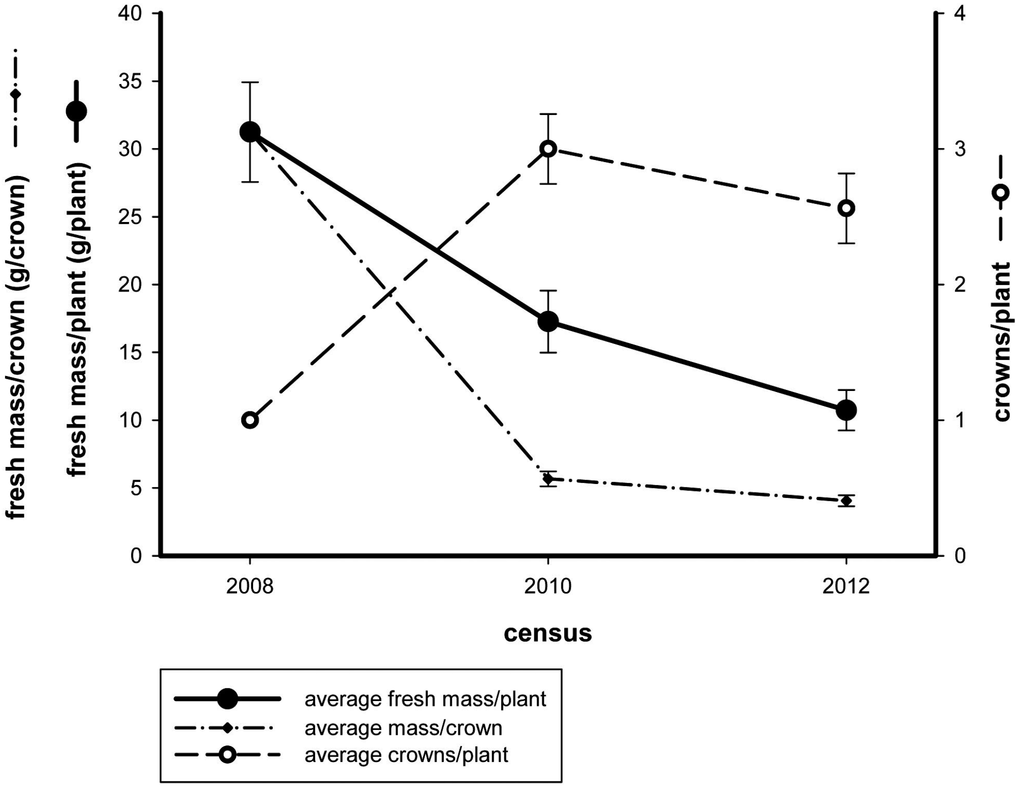

Fig. 2. Average fresh above-ground mass per harvested plant, number of crowns per plant, and average fresh mass per crown at each date. To calculate average fresh mass per crown, an average was calculated for all crowns of each plant, and then those values were averaged. Only multiple-harvest plants were used to calculate the values in this graph. Vertical bars: 1 standard error.

stantially more rain (32.4 cm October–March precipitation) than the six months periods preceding the other two censuses (6.0 cm and 15.4 cm October–March precipitation preceding the 2008 and 2012 censuses, respectively; U.S. Department of Agriculture 2012), but the average size of control plants declined in the first interval and increased in the second (Fig. 4). However, it may be that in wetter years peyote experiences more competition from other plants that have responded rapidly to the increased soil moisture. Harvesting also significantly, and strongly, affected plant growth rate and therefore plant size (Fig. 4). Each harvest reduced plant growth rates. The 2008 harvest reduced the average growth rate of all harvested plants (Terry et al. 2011). The 2010 harvest of the multiple-harvest plants significantly reduced their growth rate below that of the single-harvest plants (harvested only in 2008) as well as below the growth rate of the never-harvested control plants (Fig. 4). While the single-harvest plants and the controls had about the same growth rate between 2010 and 2012, the single-harvest plants were so much smaller in 2010 (due to the 2008 harvest) that they remained much smaller than the control plants in 2012. Meanwhile, the multiple-harvest plants continued to decline in size between 2010 and 2012. Plant size and plant survival are usually highly correlated (Harper 1977), so we expect to see continuing excess mortality of the multiple-harvest plants.

There are probably several reasons why harvesting reduces growth rate, size and survival rate. Microbial infection of the open wound created by the act of harvesting the crown of a plant, for example, cannot be ruled out. But one mechanism that appears to be an inevitable consequence of harvesting is that of exhaustion due to prolonged deprivation of solar energy. The crown, being the only aerial organ of the peyote plant, is the plant's

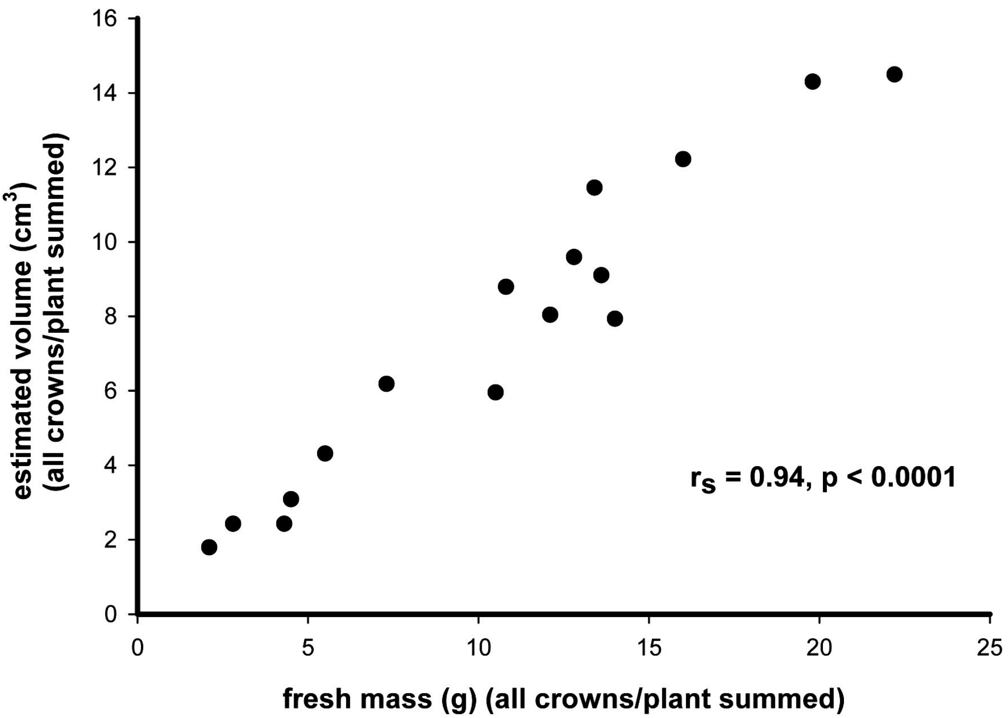

Fig. 3. Measured fresh mass and estimated volume of plants harvested from multiple-harvest peyote plants in 2012. Each point represents one plant. The volume of each crown was estimated as a hemisphere with radius equal to half the measured diameter of the crown, and then these volumes were summed to obtain plant volume. Crown masses were summed to obtain the above-ground mass of each plant.

only site of photosynthesis. Without photosynthesis, the plant cannot use solar energy to create and store carbohydrates, and nutrient, carbon, and water uptake are greatly reduced. The crown is also the part of the plant that is always harvested for ceremonial use. When the crown is harvested—thereby becoming a button in the peyote trade—the plant's ability to photosynthesize is ipso facto reduced to zero. The harvested plant then uses stored energy, nutrients, and water to regrow its above-ground biomass. If reharvesting occurs before the plant has had time to rebuild its stored reserves from photosynthesis in its regrown above-ground tissue, it will become successively smaller at each harvest and eventually die. The reduced size and growth rate, and increased mortality, of harvested plants strongly support the hypothesis that a two-year cycle of harvesting of this species is too frequent for plant recovery. A sustainable frequency of harvesting would be low enough to allow a plant to fully regrow and to fully rebuild its supply of stored resources between harvests. We hope eventually to be able to determine the maximum sustainable harvesting frequency. Whatever that frequency may be, our data indicate that harvesting on a two-year cycle is too frequent to be sustainable.

As is true of most plant species, the removal of the apical meristem (part of the harvested crown of peyote), in addition to stimulating regrowth, probably also de-represses axillary meristems, resulting in the formation of multiple crowns. In the absence of the continual secretion by the apical meristem of the hormone that normally suppresses lateral branching (presumably auxin, based on Mauseth and Halperin 1975), one (or more) of the axillary meristems in the areoles on the subterranean portion of the stem is de-repressed and begins to form a new crown at the apex of a lateral branch which emerges from the subterranean stem and grows toward the surface of the ground. This phenomenon accounts for harvested plants of this species having more crowns than unharvested plants (Fig. 2). It is a temporary phenomenon, however, because eventually a plant's stored resources are exhausted by too frequent harvesting, causing the number of crowns per plant to de-

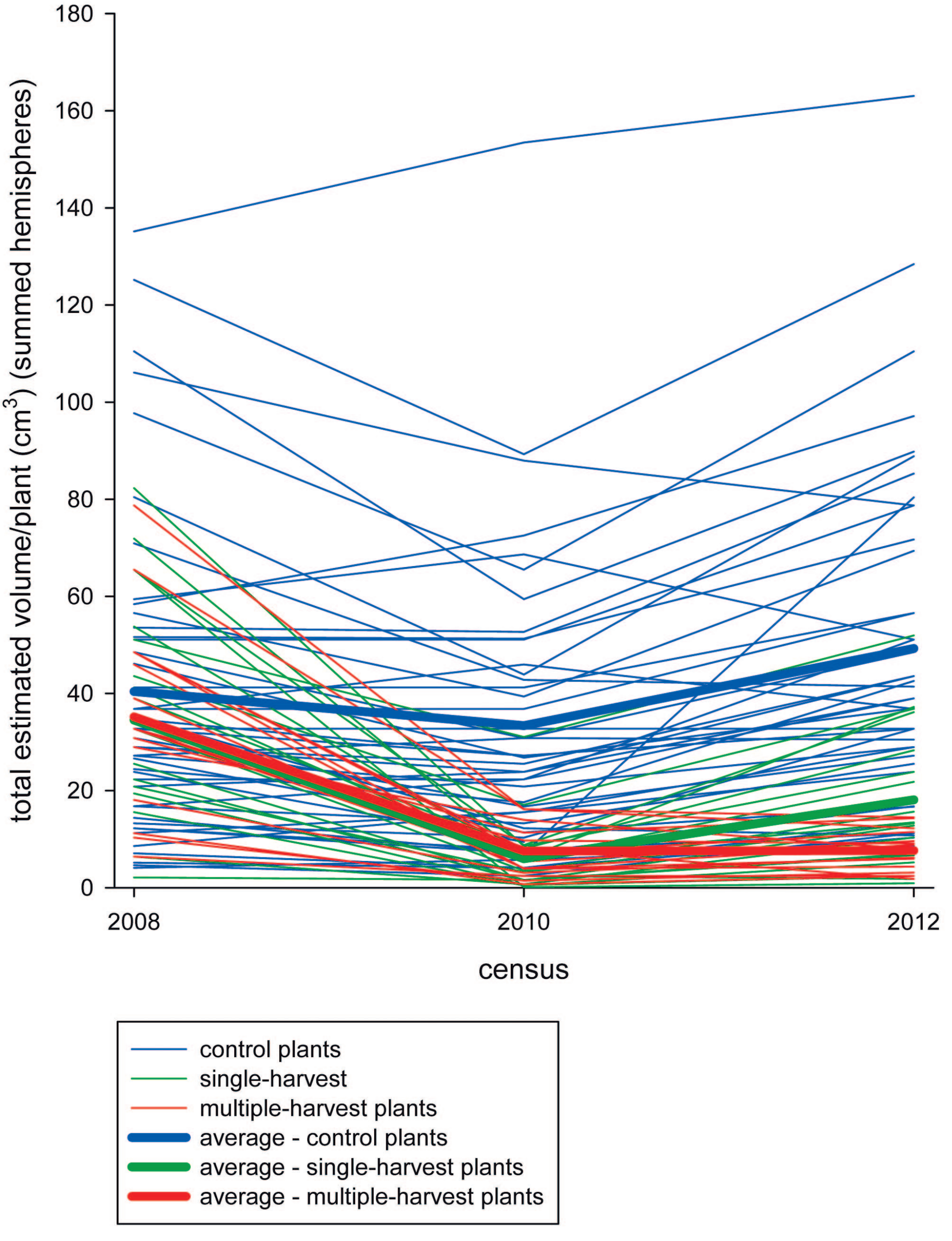

Fig. 4. Estimated above-ground volume per plant over time. Each thin line represents one plant. The volume of each crown was estimated separately, and then these volumes were summed for each plant separately, on each date separately. Control plants are blue, single-harvest plants are green, and multiple-harvest plants are red. The thick lines are averages for each treatment, using the same colors, and calculated by averaging estimated plant volumes. For simplicity, this graph has averages of untransformed values and a linear y-axis scale, but the statistical analysis used log-transformed data.

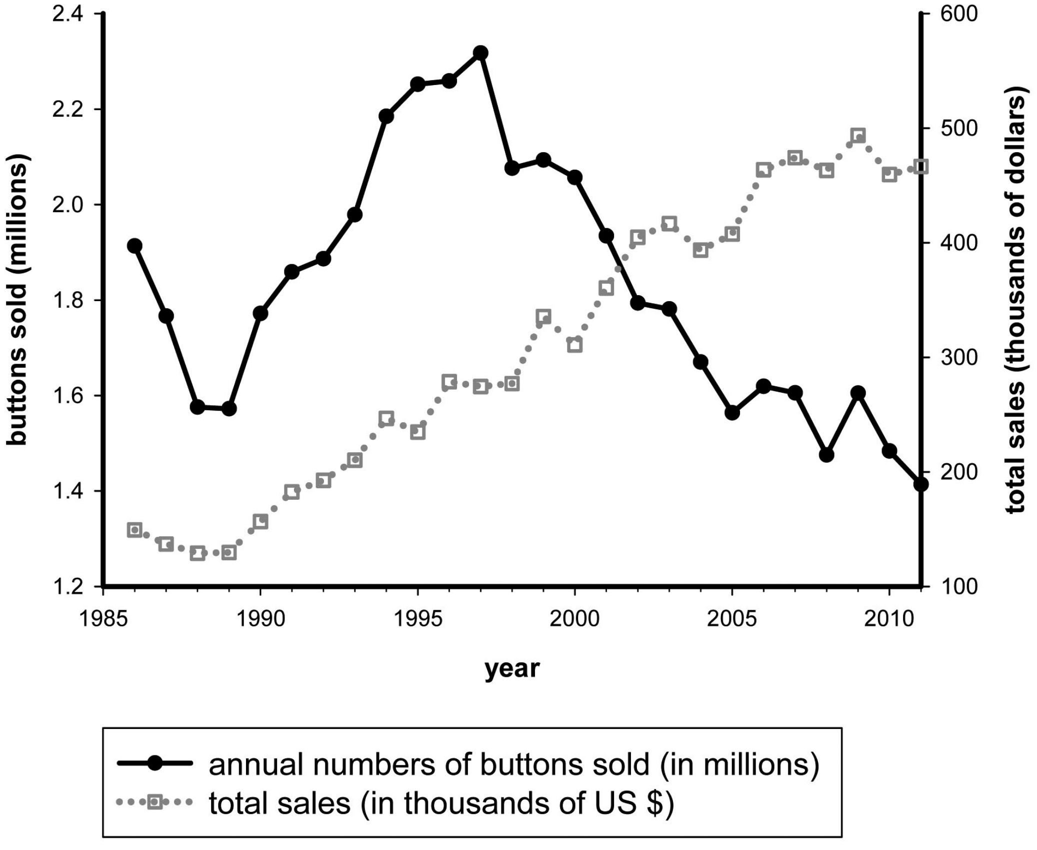

Fig. 5. Annual peyote sales by licensed distributors in South Texas from 1986 through 2011.

crease. This stage appeared to be reached at the second harvest: the number of crowns per plant increased after the first harvest but declined after the second.

The negative impact of harvesting will be greater if portions of the subterranean stem are also removed. To avoid such damage to the harvested plants, in this study we used only best harvesting practices, viz., cutting the crown at its base, parallel to the surface of the ground. However, commercial harvesting practices may remove a substantial portion of the subterranean stem along with the crown (Terry & Mauseth 2006). Such removal of subterranean stem tissue reduces the number of areoles available to initiate lateral branching, reducing the number of new crowns that can be formed. In addition it removes even more resources from the plant, reducing the amount available for regrowth.

Changes in harvest yield over time

As a result of the effects of harvesting on plant size, the yield per plant of harvested biomass decreased after each biennial harvest, first by 44% and then by 32% (Fig. 2, solid line). If one includes mortality in these calculations, the decrease in harvest yield is even more marked: the third harvest produced only 25% of the biomass that the first harvest did. For example, if we had begun with 100 plants, the first harvest would have yielded 3125 g (i.e., 100 plants × 31.25 g/plant), the second harvest would have yielded 1547 g (100 plants × 0.895 survival rate of harvested plants 2008–2010 × 17.27 g/plant), and the third harvest would have yielded 769 g (100 plants × 0.895 × 0.800 survival rate 2010–2012 × 10.73 g/plant), declines of about 50% per harvest. The absolute (as opposed to relative) decline was smaller in the second two-year period, but only because it began from a lower baseline. These are exactly the effects on harvest yield to be expected if harvesting is occurring too frequently for plants to regrow and to rebuild their stored resources.

The fact that harvested mass was even more closely correlated with estimated volume at census 3 (Fig. 3) than at census 2 (Fig. 3 in Terry et al. 2011) may seem surprising in that the crowns of most adult peyote plants do not appear to have a true hemispherical shape, but rather the shape of half of an oblate sphere. However, many of the younger plants—and especially young regrowth crowns—do indeed have vertically extended crowns, and all peyote plants tend to expand vertically in response to rain (MT, pers. obs.), which would tend to balance out the more flattened shape of the adults and the flattening effect of drought, over time.

Peyote as a classic case of overharvesting?

Peyote shows many of the hallmarks of a classic case of unsustainable harvesting of a wild resource. First, the decline in total harvest combined with an increase in price/unit is characteristic of overharvested wild species (cf. Fig. 1 in Schippman et al. 2002). A declining number of wild plants is a likely explanation for the failure of the harvest to increase in response to the increase in unit price (because a declining population causes decreases in "catch" per unit of harvesting effort, so that increasing the harvest is financially unrewarding even if there are still individuals to be harvested (Hilborn & Walters 1992; Thurstan et al. 2010). Second, there are anecdotal reports of declining unit (button) size (TH, pers. obs.). Declining body size is another classic indicator of overharvesting (Stergiou 2002; Berkeley et al. 2004; Genner et al. 2010). Third, there are anecdotal reports of declining quality of the harvested buttons (TH, pers. obs.). Fourth, the harvesting frequency (every other year) shown to be unsustainable by the present study is typical. Finally, our results may underestimate impacts of harvesting, as our harvests may have been less damaging to individual plants than a commercial harvest, due to the care taken in the harvests of this study.

As far as we are aware, this study is the first well documented case of overharvesting of a cactus species (but see Jiménez-Sierra and Eguiarte 2010, in which browsing was also involved). It is also one of a limited number of well documented cases of overharvesting of non-timber plant species in general. Most well documented cases of overharvesting of wild resources involve marine and freshwater animal species (Jackson et al. 2001; Allen et al. 2005; Genner et al. 2010). There are detailed reports of overharvesting of many tree species (e.g., Schwartz et al. 2002; Schulze et al. 2008). There are some detailed reports of overharvesting of herbaceous plant species, of which ginseng (*Panax quinquefolius*) is perhaps the best documented (Nantel et al. 1996; McGraw 2001; Case et al. 2007; McGraw et al. 2010). However, many hundreds (at least) of other plant species are threatened by overharvesting, especially plant species harvested for medicinal uses (Schippman et al. 2002), for lumber (Oldfield et al. 1998), or for collectors (Oldfield 1997).

The regulatory panorama

At the moment there are only two major interested parties with any standing in the discussion about the fate of peyote in its natural habitat: (1) the Native American Church (NAC), whose right to consume peyote for religious purposes is protected by legislation such as the American Indian Religious Freedom Act (AIRFA), and (2) the Drug Enforcement Administration (DEA), which is obligated by the Controlled Substances Act to regulate the use and distribution of peyote by and for the NAC, and to prevent the diversion of peyote to non-authorized persons. Neither of these parties is speaking very audibly about regulatory solutions to mitigate the deteriorating state of the wild peyote populations. This is unfortunate, as the problem has a feasible solution, namely the regulated cultivation of peyote by and for the NAC, which would reduce the harvesting pressure on the wild populations (as in, e.g., Kay et al. 2011). Furthermore, this solution is technically within reach (Chandra et al. 2006) and culturally acceptable (TH, pers. obs.). The barrier to bringing this solution to fruition is essentially a regulatory one. Cultivation of *L. williamsii* is anticipated in the American Indian Religious Freedom Act (as amended 1994), which "…does not prohibit such reasonable regulation and registration by the Drug Enforcement Administration of those persons who cultivate…peyote…." But to date no interested party (e.g., the NAC of North America) has petitioned the DEA to promulgate any such "reasonable regulation" spelling out the details for such registration. Pending such action, cultivation of peyote, though not illegal, lacks the needed regulatory framework to provide legal certainty and protection for NAC members who would prefer to produce their own sacrament by cultivation rather than continuing to overharvest the wild populations. Until such time as the NAC and the DEA negotiate specific regulations to govern cultivation, the harvesting pressure on the wild populations can only increase.

But let us assume that the current level of unsustainable harvesting pressure is maintained, and that populations of peyote continue to produce steadily decreasing yields, as demonstrated in this study and in the regulated peyote market. Under the current system—which can accurately be described as "management by extirpation"—at some point the conservation crisis will become so critical that the U.S. Fish and Wildlife Service will be obligated by the terms of the Endangered Species Act to evaluate the conservation status of the species *Lophophora williamsii*. At that point the regulatory situation will become substantially more complex. If a regulatory stalemate then ensues, the NAC's options may broaden (or narrow) to include the Supreme Court and/or Congress as sources of relief.

ACKNOWLEDGMENTS

We are most grateful to C.W. Hellen Ranches, Ltd. – La Mota Division – Charles W. (Bill) Hellen, Managing Partner, for providing access to his ranch and good company. We also thank the younger generations of the Herrera and Terry families for their help with the hard labor involved in the logistics of conducting the study. Garry Stephens kindly provided USDA Field Office climate data for Hebbronville, Texas. Essential funding for the study was generously provided by Libbie and Jerald Mize, the Alvin A. and Roberta T. Klein Foundation, Sul Ross State University (in the form of a Research Enhancement grant), and all the donors supporting the scientific work of the Cactus Conservation Institute, Inc. We appreciate the helpful comments of Michael Powell, James Weedin, and Patrick Griffith in their reviews of the manuscript.

REFERENCES

Allen, J.D., R. Abell, Z.E.B. Hogan, C. Revenga, B.W. Taylor, R.L. Welcomme, and K. Winemiller. 2005. Overfishing of inland waters. Bioscience 55:1041–1051.

Anderson, E.F. 1995. The "Peyote Gardens" of South Texas: A conservation crisis? Cact. Succ. J. (U.S.) 67:67–73.

Anderson, E.F. 1996. Peyote: The divine cactus. University of Arizona Press, Tucson.

Berkeley, S.A., M.A. Hixon, R.J. Larson, and M.S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29:23–32.

Case, M.A., K.M. Flinn, J. Jancaitis, A. Alley, and A. Paxton. 2007. Declining abundance of American ginseng (*Panax quinquefolius*) documented by herbarium specimens. Biol. Conservation 134:22–30.

Chandra, B., L. Palni, and S. Nandi. 2006. Propagation and conservation of *Picrorhiza kurrooa* Royle ex Benth.: an endangered Himalayan medicinal herb of high commercial value. Biodivers. & Conservation 15:2325–2338.

Fitz Maurice, B. and W.A. Fitz Maurice. 2009. *Lophophora williamsii*. In: IUCN, ed. 2012. IUCN Red List of Threatened Species. Version 2012.1. <www.iucnredlist.org>. Accessed: 28 June 2012.

Genner, M.J., D.W. Sims, A.J. Southward, G.C. Budd, P. Masterson, M. McHugh, P. Rendle, E.J. Southall, V.J. Wearmouth, and S.J. Hawkins. 2010. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. Global Change Biol. 16:517–527.

Harper, J. 1977. Population biology of plants. Academic Press, London.

Hilborn, R. and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.

Jackson, J.B.C., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi, C.H. Peterson, R.S. Steneck, M.J. Tegner, and R.R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637.

Jiménez-Sierra, C. and L. Eguiarte. 2010. Candy barrel cactus (*Echinocactus platyacanthus* Link & Otto): a traditional plant resource in Mexico subject to uncontrolled extraction and browsing. Econ. Bot. 64:99–108.

Kay, J., A. Strader, V. Murphy, L. Nghiem-Phu, M. Calonje, and M.P. Griffith. 2011. Palma Corcho: a case study in botanic garden conservation horticulture and economics. HortTechnol. 21:474–481.

Mauseth, J.D. and W. Halperin. 1975. Hormonal control of organogenesis in *Opuntia polyacantha*. Amer. J. Bot. 62:869–877.

McGraw, J.B. 2001. Evidence for decline in stature of American ginseng plants from herbarium specimens. Biol. Conservation 98:25–32.

McGraw, J.B., S. Souther, and A.E. Lubbers. 2010. Rates of harvest and compliance with regulations in natural populations of American ginseng (*Panax quinquefolius* L.). Nat. Areas J. 30:202–210.

Nantel, P., D. Gagnon, and A. Nault. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. Conservation Biol. 10:608–621.

NatureServe. 2012. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. Available at http://www.natureserve.org/explorer (Accessed: July 3, 2012.)

Oldfield, S. (ed). 1997. Cactus and succulent plants—Status survey and conservation action plan. IUCN/SSC Cactus and Succulent Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Oldfield, S., C. Lusty, and A. MacKinven. 1998. The world list of threatened trees. World Conservation Press, Cambridge, UK.

Powell, A.M., J.F. Weedin, and S.A. Powell. 2008. Cacti of Texas: a field guide. Texas Tech University Press, Lubbock.

Schippmann, U., D.J. Leaman, and A.B. Cunningham. 2002. Impact of cultivation and gathering of medicinal plants on biodiversity: global trends and issues. In: Departmental Working Group on Biological Diversity for Food and Agriculture, FAO (ed). Biodiversity and the Ecosystem Approach in Agriculture, Forestry and Fisheries. Satellite event on the occasion of the Ninth Regular Session of the Commission on Genetic Resources for Food and Agriculture. Rome, 12–13 October 2002. FAO, Rome. Available at http://www.fao.org/DOCREP/005/AA010E/AA010E00.HTM

Schulze, M., J. Grogan, C. Uhle, M. Lentini, and E. Vidal. 2008. Evaluating ipê (*Tabebuia*, Bignoniaceae) logging in Amazonia: sustainable management or catalyst for forest degradation? Biol. Conservation 141:2071–2085.

Schwartz, M.W., T.M. Caro, and T. Banda-Sakala. 2002. Assessing the sustainability of harvest of *Pterocarpus angolensis* in Rukwa Region, Tanzania. Forest Ecol. Managem. 170:259–269.

Stergiou, K.I. 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. Fish. Res. 55:1–9.

Terry, M. 2008a. Stalking the wild *Lophophora*. Part 1. Chihuahua and Coahuila. Cact. Succ. J. (US) 80:181–186.

Terry, M. 2008b. Stalking the wild *Lophophora*. Part 2. Zacatecas, San Luis Potosí, Nuevo León, and Tamaulipas. Cact. Succ. J. (U.S.) 80:222–228.

Terry, M. 2008c. Stalking the Wild *Lophophora*. Part 3. San Luis Potosí (central), Querétaro, and Mexico City. Cact. Succ. J. (U.S.) 80:310–317.

Terry, M. and J.D. Mauseth. 2006. Root-shoot anatomy and post-harvest vegetative clonal development in *Lophophora williamsii* (Cactaceae: Cacteae): implications for conservation. Sida 22:565–592.

Terry, M., K. Trout, B. Williams, T. Herrera, and N. Fowler. 2011. Limitations to natural production of *Lophophora williamsii* (Cactaceae) I. Regrowth and survivorship two years post harvest in a South Texas population. J. Bot. Res. Inst. Texas 5:661–675.

Texas Department of Public Safety. Peyote sales data. Unpublished.

Thurstan, R.H., S. Brockington, and C.M. Roberts. 2010. The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nature Commun. 1:15.

Trout, K. 1999. Sacred cacti. Second Edition. Better Days Publishing, Austin.

U.S. Department of Agriculture. 2012. USDA Field Office Climate Data for WETS Station at Hebbronville, Texas.