REGENERATION OF *LOPHOPHORA WILLIAMSII* (CACTACEAE) FOLLOWING MUMMIFICATION OF ITS CROWN BY NATURAL FREEZING EVENTS, AND SOME OBSERVATIONS ON MULTIPLE STEM FORMATION

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ABSTRACT

Exposure of *Lophophora williamsii* to environmental temperatures that remained continuously below freezing, with lows estimated at or below −10 to −15°C for three consecutive days, resulted in freeze-drying of the crowns of some individuals in their natural habitat. I dug up one such plant, brought it back to the lab, planted it in a pot, watered it weekly, and monitored it for signs of life. Eight weeks later new growth was observed as incipient lateral branches from the meristems at areoles on the subterranean portion of the stem. Eleven weeks after replanting and watering, there were four such offsets on the plant. This recovery attests to the resilience of this species in the face of extreme environmental conditions. It also shows that prolonged freezing under dry conditions constitutes a natural mechanism for destruction of the apical meristem. Such meristem destruction by frost would have the same effect on lateral branching as removal of the apical meristem by human harvesting of the crown, and thus provides an alternative mechanism for the formation of pseudocespitose clusters of densely packed individuals in habitat. The concepts of cespitosity (multiple stems on a single plant) and pseudocespitosity (multiple individuals in a dense cluster) are discussed with examples. *Phytologia 93(3): 330-340 (December 1, 2011)*

KEY WORDS: *Lophophora*, peyote, cold tolerance, apical meristem, subterranean areoles, lateral branching, regeneration, cespitose.

During the interval of 2−5 Feb 2011, the Big Bend region of Trans-Pecos Texas experienced a hard freeze which in many areas had the longest continuous duration of sub-freezing temperatures in living memory (A.M. Powell, pers. comm.). This freeze occurred five months into a drought during which no biologically significant precipitation had occurred. A population of *Lophophora williamsii* (Lem. ex Salm-Dyck) J.M. Coult. (peyote) in southern Presidio County was adversely affected by the combination of drought and frost (pers. obs.).

Drought is a frequent phenomenon in Trans-Pecos Texas, and the *Lophophora* plants respond to it by contraction of the root (and possibly the underground portion of the stem, which may be substantially larger in volume than the root). This contraction pulls the crown of the plant down to, or even below, ground level, thus reducing its exposure to the evaporative forces of sun and wind (Fig. 1), as has been documented in *Ariocarpus fissuratus*, a sympatric cactus similar in habit and habitat to *L. williamsii* (Garrett et al., 2010).

The hard freeze of Feb 2011, however, was no ordinary occurrence. According to weather records for Presidio, Texas (U.S. Border Patrol, unpublished data), beginning the night of 2 Feb, the temperature remained at or below freezing continuously until the afternoon of 5 Feb, and the low temperatures in this interval were −9ºC on 3 Feb, −14º on 4 Feb, and −14º on 5 Feb. The altitude of Presidio is ca. 800 m. The *L. williamsii* specimens that suffered frost damage were at ca. 1300 m in the vicinity of the Chinati Mountains. That difference in altitude virtually ensures that the temperatures experienced by the population of *L. williamsii* were lower than the temperatures recorded at Presidio. Also associated with the higher altitude would be a lower atmospheric pressure, which would have increased the rate of sublimation of ice to water vapor, thus enhancing the lyophilizing effect of the cold dry air. The combination of the extreme low temperatures and the extreme duration of those low temperatures made this the most intense cold-weather event on record for this region.

MATERIALS AND METHODS

On 24 Apr 2011, a typical eight-ribbed adult *L. williamsii* specimen measuring ca. 5 cm in diameter and growing in calcareous soil on an exposed natural terrace near the top of a slope was carefully dug up so as to cause minimal damage to the distal portion of the taproot and to the lateral roots. The individual was selected because, as with approximately 3−5% of the plants in the population, its crown had evidently been completely freeze-dried by the prolonged hard freeze of early February. Whereas in a normal *L. williamsii* specimen in the same population the crown would consist of raised, soft parenchyma tissue covered with gray-green dermal-epidermal tissue (Fig. 1), in the case of the frost-damaged specimen the crown had been reduced to a thin layer of hard dry tissue of light reddish brown color and of the consistency of solid wood (Figs. 2a, 2b, 2c). This frost-damaged specimen retained a high density (due to high water content) in its subterranean stem and root, which suggested that the plant could be alive. Therefore it was brought back to the greenhouse, replanted in a pot, watered weekly, and monitored for signs of life.

RESULTS AND DISCUSSION

On 16 Jun 2011, ca. 8 weeks after the specimen was replanted in the greenhouse, three offsets were visible above ground level, and by 7 Jul 2011 (ca. 11 weeks after replanting) a fourth offset had appeared above ground level (Fig. 3). Offsets are lateral branches produced by areolar meristems on the subterranean stem in response to death or removal of the apical meristem at the center of the crown of the cactus. The production and development of such lateral branches as a consequence of human harvesting of peyote is described and photographically documented by Terry and Mauseth (2006). Commercial peyote harvesting typically involves cutting the crown off at such a depth as to effect the removal of the apical meristem of the harvested plant. The lateral branches produced as a result (due to derepression of branching as a consequence of removal of the apical meristem, which is the source of branch-suppressant auxins) emerge from the ground as small crowns around the perimeter of the decapitated parent plant (Fig. 4), and eventually mature into independent plants that ultimately detach themselves from the degenerating body of the parent plant (Terry and Mauseth, 2006).

A problem arises in field interpretation of close clusters of crowns of *L. williamsii*. By definition a cespitose individual has a central "parent" stem, which has produced multiple lateral branches, each of which bears a crown, and each of these lateral branches in turn may give rise to multiple lateral branches with their own crowns. Thus the key criterion for a cespitose plant is that all crowns are connected by living tissue (particularly vascular tissue) to the central parent stem; i.e., a cespitose plant is a single plant with multiple stem branches (Powell and Weedin, 2004). The problem lies in distinguishing a cespitose plant from a dense cluster of unconnected – but often contiguous – individual plants; such a cluster can be characterized as pseudocespitose. The mechanisms for the development of such pseudocespitose clusters of individual plants include the following:

(1) The plants all germinated from seeds produced by a parent plant or plants, living or long dead. The adults that develop from such seeds are then simply separate individual plants that happened to germinate very close to the parent plant, and hence very close to each other, which is a frequent occurrence in cultivation, where *L. williamsii* is a copious seed producer (pers. obs.).

(2) The crown of the original parent plant was harvested by humans who removed the apical meristem along with the crown (or “button”), whereupon lateral branching produced new crowns which put down their own adventitious taproots and ultimately became independent of the parent stem, which eventually degenerated and died (as in Fig. 4, where the harvesting occurred per the protocol of a controlled study of the effects of harvesting: Terry et al., unpublished data).

(3) The crown of the original plant was killed, or the apical meristem was destroyed without necessarily killing the crown, by some environmental insult, such as undergoing severe frostbite and/or lyophilization as described above, or simply being stepped on by an ungulate. The progression of subsequent events would be essentially identical to those caused by harvesting – since the critical event is the loss of the apical meristem, regardless of the

specific cause of such loss – and the end result will likewise be the death and disappearance of the parent plant, leaving a dense cluster of independent clonal progeny occupying the spot where the parent plant had been.

This is not to imply that true cespitose *Lophophora* plants do not exist. On the contrary, in the early stages of the progression of events following loss of the apical meristem, every damaged parent plant undergoing the transition to a pseudocespitose cluster of independent clonal progeny plants must first go through a true cespitose phase, where the new crowns borne on lateral branches are not yet independent of the parent plant that lost its apical meristem. And if we broaden the taxonomic and geographic scope beyond *L. williamsii* in U.S. populations – and consider, for instance, the clump-forming habit of *L. fricii* growing in the Laguna de Viesca in Coahuila (Fig. 5; Terry, 2008a), *L. diffusa* in Querétaro (Fig. 6; Terry, 2008b), and indeed *L. williamsii* at Miquihuana, Tamaulipas (Fig. 7), and El Huizache, San Luis Potosí, Mexico (Fig. 8), as documented by Anderson (1969) and Terry (2008c and 2008b, respectively) – then we see what appear to be clear and impressive instances of cespitosity. However, the only way to be certain as to whether a multi-crowned *Lophophora* specimen (such as the specimen(s) from Terrell County, Texas, in Fig. 9) is cespitose or pseudocespitose, is to dig it up and look at the subterranean architecture of the plant(s) to see if the densely growing crowns are interdependent or if some are independent of the others. The destructiveness of such excavation, particularly in the case of what we infer to be very old clumps of cacti of vulnerable taxa, may be deemed too high a price to pay for scientific knowledge.

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LITERATURE CITED

Anderson, E.F. 1969. The biogeography, ecology, and taxonomy of *Lophophora*, (Cactaceae). Brittonia 21: 299−310.

Garrett, T. Y., Huynh, C.-V., and North, G. B. 2010. Root contraction helps protect the "livng rock" cactus from lethal high temperatures when growing in rocky soil. Amer. J. Bot. 97: 1951−1960.

Powell, A. M. and Weedin, J. F. 2004. Cacti of the Trans-Pecos and Adjacent Areas. Texas Tech University Press, Lubbock.

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

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

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

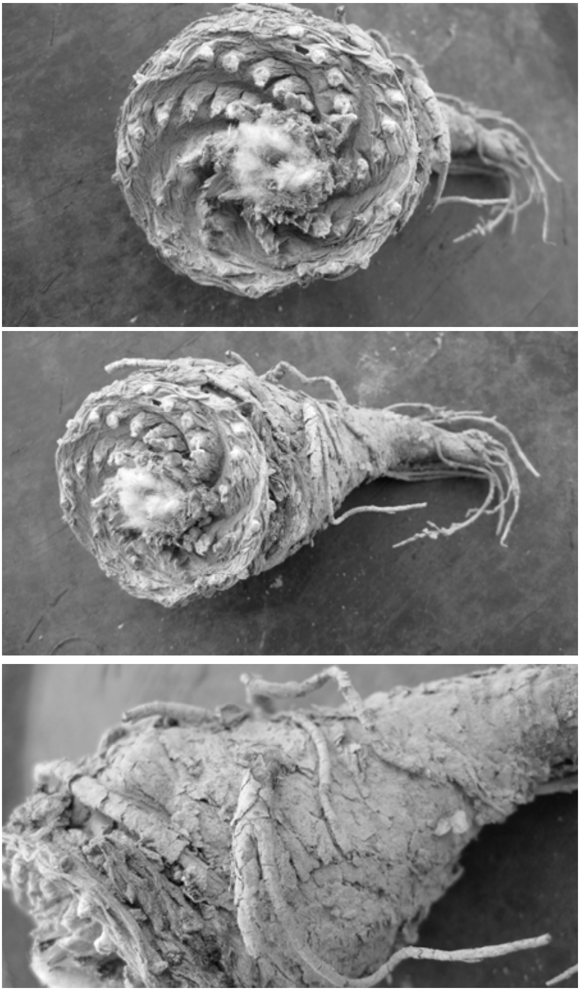
Terry, M., Mauseth, J. D. 2006. Root-shoot anatomy and post-harvest vegetative clonal development in *Lophophora williamsii* (Cactaceae: Cacteae): Implications for conservation. Sida 22: 565−592.

Fig. 1. Typical healthy specimens of *Lophophora williamsii* in habitat in Presidio County, Texas.

Fig. 2a.

Fig. 2b.

Fig. 2c.



Figs. 2a, 2b, and 2c. Specimen of *L. williamsii* whose crown underwent natural lyophilization in the cold, dry, somewhat high-altitude environment of the Big Bend region during the prolonged hard freeze of 2−5 Feb 2011.

Fig. 3. Four new offsets ("pups") that emerged after transplanting the specimen shown in Fig. 1 to a pot in the greenhouse and providing water for 11 weeks. The emergence of offsets indicates that the plant is alive but its apical meristem is dead.

Fig. 4. Four offsets from a decapitated subterranean stem of a *L. williamsii* plant harvested in habitat three years previously in Jim Hogg County, Texas. Such regrowth in the form of lateral branches represents the typical response to harvesting in this species.

Fig. 5. A large clump of *L. fricii* growing in the Laguna de Viesca in Coahuila, Mexico.

Fig. 6. A typical clump of *L. diffusa* growing near a dry creekbed in Querétaro, Mexico.

Fig. 7. A clump of *L. williamsii* growing west of Miquihuana in southern Tamaulipas, Mexico.

Fig. 8. A relatively small clump of *L. williamsii* growing at El Huizache, in San Luis Potosí, Mexico.

Fig. 9. A clump of *L. williamsii* growing in Terrell County, Texas. The question goes begging as to whether it is a cespitose individual or a pseudocespitose cluster of individuals.

Note: The photographs for Figures 1-9 can be viewed in color at: http://www.cactusconservation.org/CCI/Lwfreezedry.html