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Author: Killingbeck, Keith T.

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TWO DISTINCT GROWTH FORMS OF THE ICONIC DESERT SHRUB OCOTILLO (*FOUQUIERIA SPLENDENS*): *TARANTULA* AND *V-FORM*

KEITH T. KILLINGBECK

Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881
keith@uri.edu

ABSTRACT

The discovery of an atypically shaped Ocotillo (*Fouquieria splendens* Englem.) at one of my research sites in the foothills of the Organ Mountains in southern New Mexico led to a study to determine whether this was an oddity or a recurring growth form. Ocotillo, the iconic C3, drought-deciduous desert shrub of the Chihuahuan and Sonoran Deserts, typically appears as a multistemmed, spine-laden shrub described as having the appearance of an inverted cone. The new growth form introduced here departed markedly from the V-shape so often associated with Ocotillo. The new growth form, termed *Tarantula* because its stems are reminiscent of the low, arching legs of the spider, is characterized by having a) a ratio of <0.8 between the maximum height above ground of its longest stem and the maximum length of the same stem, b) an angle between the longest stem and the ground of $<50^\circ$, and c) stems with a horizontal or downward arching curvature. In 71 transects distributed across four states in the United States and two states in Mexico, 8% of the 6739 Ocotillos sampled were the *Tarantula* growth form. The mean percentage of *Tarantula* plants per transect was 8.9%. Six hypotheses are offered as potential explanations for the atypical architecture of the *Tarantula* growth form. That none of these hypotheses provided a definitive explanation indicates that this visually distinct, widely distributed variant of *Fouquieria splendens* merits further study. Three avenues of future research are suggested.

Key Words: Chihuahuan Desert, desert shrubs, *Fouquieria splendens*, Ocotillo, Sonoran Desert.

Ocotillo (*Fouquieria splendens* Englem.), the iconic C3, drought-deciduous shrub of the Chihuahuan and Sonoran Deserts, is often described as having “wandlike, ascending stems” (Turner et al. 1995) that collectively form “inverted cones” (Benson and Darrow 1944). Shreve (1917) more precisely described Ocotillo stems as consisting of “straight unbranched limbs ... at an angle of 30 to 70° from the ground.” Given that each assemblage of spine-laden stems emerges from a “short, broad basal trunk” (Henrickson 1972) that is often not discernable from a distance, the overall architecture of Ocotillo is indeed that of an upright ‘V.’ So common is this visual impression of the species that Cornett (2017) has deemed it “ocotillo’s splendid uniformity of form.”

Early on in my studies of Ocotillo in the foothills of the Organ Mountains in southern New Mexico, I noticed an Ocotillo that departed markedly from the V-shape so often associated with this species (Fig. 1). Added to that observation was the presence of an Ocotillo several meters away that perfectly matched the typical inverted cone form of the species. What could possibly cause such a difference in adjacent plants, and was this a unique oddity or something more common? After noticing the occurrence of both forms of Ocotillo at wide-ranging sites and finding that there was nothing in the literature describing the previously undescribed form, I began a search for populations of Ocotillos in the North American Southwest to determine the frequency and distribution of both forms of Ocotillo.

I opted against using ‘normal’ and ‘atypical’ as labels for the two growth forms because these terms are not descriptive, and ‘normal’ implies a judgment that I wished to avoid. Instead, the names that emerged were *V-form* for the inverted cone shape most often used to describe Ocotillo architecture, and *Tarantula* for the low growth form with arching stems reminiscent of the body and legs of the tarantula spider.

Seventy-one transects geographically distributed among four states in the United States and two states in Mexico were sampled from 1999–2016 to determine the occurrence, distribution, and relative frequency of *Tarantula* Ocotillos within the typically *V-form*-dominated populations of Ocotillo in the North American Southwest.

METHODS

The original observation of the atypical growth form of Ocotillo took place in 1986 in the foothills of the Organ Mountains in southern New Mexico at a site established for other Ocotillo research ($32^\circ 19'N$, $106^\circ 38'W$). A brief site description can be found in Killingbeck (2019). Since 2014, the site has become part of the Organ Mountains-Desert Peaks National Monument. I will use the common name ‘Ocotillo’ to refer to *Fouquieria splendens* even though that name is applied to additional species of *Fouquieria* in Mexico.

After the initial observation of the *Tarantula* Ocotillo and additional observations elsewhere confirming the existence of this growth form in other



FIG. 1. Two growth forms of Ocotillo (*Fouquieria splendens*) next to one another in the foothills of the Organ Mountains outside of Las Cruces, NM. The *Tarantula* type is on the left and the *V-form* type is on the right, both growing on the same desert pavement soils. Photo from 28 May 2009 by Keith Killingbeck.

Ocotillo populations beyond the Organs and beyond New Mexico, I sought to establish a metric to objectively distinguish *Tarantula* from *V-form* growth forms. The differences between the two growth forms were visually striking, but establishing an objective means to differentiate the two was essential. On 01 June 1997 along a transect in the foothills of the Organ Mountains, I sampled 32 pairs of plants, one each of the *Tarantula* and *V-form* apparent growth forms. After finding a probable *Tarantula* individual, maximum stem length, maximum distance above ground of that stem, its diameter at one half its length, and number of stems >50 cm were measured. Then, the nearest apparent *V-form* plant of similar size and number of stems was measured the same way. Also measured was the distance between the two plants. This was repeated until 32 linked pairs were sampled. These data established a ratio between the maximum height above ground and the maximum length of the same stem that would ultimately serve as the demarcation point between *Tarantula* and *V-form* growth forms.

To further characterize differences between the two growth forms, angle from the ground, length, and curvature of the longest stem on each of 20 pairs of *Tarantula* and *V-form* plants within 5 m or less of each other were measured on 29 May 1998. Plants were sampled on level ground along a west to east transect in the foothills of the Organ Mountains. Also measured were the number of stems >50 cm on each of the 40 plants and the distance between each *Tarantula* - *V-form* linked pair. To obtain the measurements needed to calculate the angle from the ground, a plumb bob was dropped from the tip of the longest stem to the ground on each plant. The vertical distance along the plumb line and the distance on the ground from the plumb bob to the trunk of the plant were measured.

Curvature was measured as the maximum deviation from straight of either an upward and/or downward curve of the longest stem of each plant. Each measurement was made perpendicular to a straight edge touching each end of a curve.

From 23 May 1999 to 03 June 2016, 71 transects were established in Mexico and the United States to determine the geographical extent of the *Tarantula* growth form, and the ratio of the two growth forms in each transect (Table 1). Transects were established as a line along a compass direction within a population of Ocotillos in which the first 100 plants within 5 m of either side of the line were scored as either *Tarantula* or *V-form*. In the seven instances when there were fewer than 100 total plants, all plants in the population were scored. In one instance, more than 100 plants were scored.

V-form plants were scored in the field as those Ocotillos with a ratio of ≥ 0.8 of the maximum height above ground of the longest stem divided by the maximum length of the same stem. *Tarantula* plants were those with a ratio of <0.8 .

Statistical analyses were all performed with JMP 12.2.0 software (SAS Institute, Cary, NC). Dispersion around the mean was always reported as the standard error, and an alpha value of 0.05 was used to infer statistical significance. Pairs of means were compared with t-tests, and multiple means were compared with Analysis of Variance coupled with the Tukey-Kramer HSD multiple means comparisons.

RESULTS

The ratio between the maximum height above ground of the longest stem and the maximum length of the same stem turned out to be an excellent metric to distinguish the two growth forms and was used throughout this study. Not only was the mean ratio significantly different (t-test, t ratio = -14.38, df = 57, $P < 0.0001$) between pairs of adjacent *Tarantula* (0.67 ± 0.01) and *V-form* (0.91 ± 0.01) plants sampled on 01 June 1997, but there was almost no overlap in the ratio between *Tarantula* (0.50–0.80) and *V-form* (0.79–1.00) plants (Fig. 2). The mean distance between these plants was 3.9 m (n = 32 pairs; range = 1.0–9.5 m). Therefore, the ratio of 0.8 between the maximum height above ground of the longest stem of a plant and the maximum length of the same stem was used as the cut-off between *Tarantula* (<0.8) and *V-form* (≥ 0.8) growth forms.

In addition to the statistically significant difference in the above ratio, data on 20 pairs of Ocotillos the following year indicated that angle from the ground, diameter of the longest stem at half its length, and upward curvature and downward curvature of the longest stem also differed significantly between *Tarantula* and *V-form* plants (Table 2; mean distance between plants was 2.9 m [range = 0.5–4.5 m]; n = 20 pairs). Stem angle ranged from 24.8 – 49.1° in *Tarantula* plants (mean = $37 \pm 1.6^\circ$) and 54.2 – 78.7° in *V-form* plants (mean = $66 \pm 1.7^\circ$). Downward

TABLE 1. NUMBERS OF *TARANTULA* AND *V-FORM* GROWTH FORMS OF *OCOTILLO* (*FOUQUIERIA SPLENDENS*) IN 71 TRANSECTS IN ARIZONA (AZ, 17), BAJA CALIFORNIA, MEXICO (BC, 9), CALIFORNIA (CA, 2), NEW MEXICO (NM, 27), SONORA, MEXICO (SO, 3), AND TEXAS (TX, 13). The majority of transects (63) held 100 plants, but 1 held more, and 7 held fewer than 100. Latitude and longitude values are only provided if taken in the field during sampling. Sampling dates are provided once for all transects sampled the same day.

| Date | Transect | Location | V-form | Tarantula |
|----------|----------|--|--------|-----------|
| 5-23-99 | 1 | 1.6 km E of Huerfano Butte, AZ | 99 | 1 |
| | 2 | 1.6 km E of Huerfano Butte, AZ | 100 | 0 |
| | 3 | 1.6 km E of Huerfano Butte, AZ | 100 | 0 |
| | 4 | 1.6 km E of Huerfano Butte, AZ | 100 | 0 |
| | 5 | Santa Rita foothills, AZ | 99 | 1 |
| | 6 | Santa Rita foothills, AZ | 99 | 1 |
| | 7 | E side of Madeira Canyon Rd, AZ | 100 | 0 |
| 5-24-99 | 8 | 2 km S of Huerfano Butte, AZ | 99 | 1 |
| | 9 | 2 km S of Huerfano Butte, AZ | 100 | 0 |
| | 10 | 2 km S of Huerfano Butte, AZ | 100 | 0 |
| | 11 | S side of highway 90 outside of Bisbee, AZ | 100 | 0 |
| | 12 | At Douglas, AZ city limits | 100 | 0 |
| 5-27-99 | 13 | E of Las Cruces, NM; 32°19.252'N, 106°37.738'W | 63 | 37 |
| 5-28-99 | 14 | S side of Peña Blanca, NM | 85 | 15 |
| | 15 | S side of Peña Blanca, NM | 82 | 18 |
| 5-28-99 | 16 | Franklin Mountains State Park, TX; W-facing slope | 94 | 6 |
| | 17 | Franklin Mountains State Park, TX; SE-facing cut bank | 80 | 20 |
| | 18 | Franklin Mountains State Park, TX; Ridge top | 71 | 29 |
| | 19 | Franklin Mountains State Park, TX; SW-facing slope | 83 | 17 |
| 5-30-00 | 20 | Sevilleta LTER site, NM; 34°13.320'N, 106°42.250'W | 83 | 10 |
| | 21 | Sevilleta LTER site, NM; 34°13.344'N, 106°42.273'W | 19 | 0 |
| | 22 | Sevilleta LTER site, NM; 34°13.365'N, 106°42.309'W | 45 | 2 |
| 6-6-02 | 23 | Sevilleta LTER site, NM; 34°13.377'N, 106°42.353'W | 105 | 13 |
| | 24 | Sierra de las Uvas, NM; 32°30.263'N, 107°09.536'W | 40 | 1 |
| | 25 | Sierra de las Uvas, NM; 32°29.726'N, 107°08.833'W | 67 | 33 |
| | 26 | Sierra de las Uvas, NM; 32°29.172'N, 107°07.365'W | 6 | 20 |
| | 27 | Sierra de las Uvas, NM; 32°29.248'N, 107°07.323'W | 91 | 9 |
| | 28 | Sierra de las Uvas, NM; 32°28.884'N, 107°07.036'W | 17 | 20 |
| | 29 | Sierra de las Uvas, NM; 32°28.783'N, 107°07.097'W | 48 | 52 |
| 5-29-03 | 30 | SE corner CA, NW of Yuma; 32°48.907'N, 114°50.293'W | 100 | 0 |
| 5-30-03 | 31 | Joshua Tree NP, CA; 33°55.647'N, 115°54.700'W | 100 | 0 |
| 5-31-03 | 32 | NW of Wikeup, AZ; 34°54.881'N, 113°39.564'W | 100 | 0 |
| 3-4-06 | 33 | S of Road Forks, NM; 32°05.332'N, 108°58.390'W | 98 | 2 |
| | 34 | Near Transect 33; lat/long missing | 96 | 4 |
| 8-21-06 | 35 | Carlsbad Caverns NP, NM; 32°11.247'N, 104°25.355'W | 98 | 2 |
| | 36 | Carlsbad Caverns NP, NM; 32°11.350'N, 104°25.498'W | 93 | 7 |
| | 37 | Carlsbad Caverns NP, NM; 32°11.326'N, 104°25.458'W | 93 | 7 |
| 8-22-06 | 38 | Sitting Bull Falls area, NM; 32°16.185'N, 104°39.980'W | 98 | 2 |
| | 39 | Sitting Bull Falls area, NM; 32°16.209'N, 104°40.089'W | 95 | 5 |
| | 40 | Sitting Bull Falls area, NM; 32°16.303'N, 104°40.102'W | 100 | 0 |
| 9-8-06 | 41 | Saguaro NP West, AZ; 32°16.632'N, 111°11.881'W | 97 | 3 |
| 9-15-06 | 42 | NW of Lake Valley, NM; 32°43.769'N, 107°35.351'W | 86 | 14 |
| | 43 | NW of Lake Valley, NM; 32°43.759'N, 107°35.275'W | 89 | 11 |
| 9-16-06 | 44 | Bishop's Cap area, NM; 32°12.310'N, 106°35.463'W | 84 | 16 |
| | 45 | Bishop's Cap area, NM; 32°12.288'N, 106°35.463'W | 87 | 13 |
| 9-28-06 | 46 | SW A Mntn., Las Cruces, NM; 32°16.993'N, 104°42.637'W | 85 | 15 |
| 10-15-06 | 47 | Organ Pipe Cactus NM, AZ; 31°57.632'N, 112°48.337'N | 98 | 2 |
| | 48 | Organ Pipe Cactus NM, AZ; 31°56.540'N, 112°48.496'W | 100 | 0 |
| 10-16-06 | 49 | Rt. 2, W of Pinacate Biosphere Reserve, Sonora (SO) Mexico (MX); 32°16.319'N, 114°06.918'W | 100 | 0 |
| | 50 | Rt. 2, W of Pinacate Biosphere Reserve, Sonora (SO) Mexico (MX); 32°15.867'N, 114°07.325'W | 100 | 0 |
| 10-16-06 | 51 | N of San Felipe, Baja California (BC), MX; 31°25.209'N, 115°02.642'W | 96 | 4 |
| 10-17-06 | 52 | S of San Felipe, N of Puertocitos, BC, MX; 30°36.083'N, 114°41.685'W | 97 | 3 |
| | 53 | S of San Felipe, N of Puertocitos, BC, MX; 30°36.048'N, 114°41.940'W | 98 | 2 |

TABLE 1. CONTINUED

| Date | Transect | Location | <i>V</i> -form | <i>Tarantula</i> |
|----------|----------|---|----------------|------------------|
| 10-18-06 | 54 | S of Puertocitos, BC, MX; 29°58.717'N, 114°32.891'W | 84 | 16 |
| | 55 | S of Puertocitos, BC, MX; 29°58.674'N, 114°32.990'W | 83 | 17 |
| 10-18-06 | 56 | S of Isla San Luis Gonzaga, BC, MX; 29°37.044'N, 114°23.778'W | 99 | 1 |
| | 57 | S of Isla San Luis Gonzaga, BC, MX; 29°37.135'N, 114°23.621'W | 98 | 2 |
| 10-19-06 | 58 | W of El Marmol, BC, MX; 29°58.207'N, 114°48.720'W | 99 | 1 |
| | 59 | W of El Marmol, BC, MX; 29°58.147'N, 114°48.858'W | 98 | 2 |
| 10-28-06 | 60 | S of Nogales, SO, MX; 30°40.665'N, 110°53.421'W | 100 | 0 |
| 10-29-06 | 61 | N of Sierra Vista, AZ; 31°47.749'N, 110°20.974'W | 100 | 0 |
| 11-20-06 | 62 | Big Bend NP, TX; 29°17.683'N, 103°29.635'W | 92 | 8 |
| | 63 | Big Bend NP, TX; 29°17.771'N, 103°29.534'W | 91 | 9 |
| | 64 | Big Bend NP, TX; 29°10.854'N, 103°35.426'W | 100 | 0 |
| | 65 | Big Bend NP, TX; 29°11.015'N, 103°35.279'W | 97 | 3 |
| | 66 | Big Bend NP, TX; 29°12.090'N, 103°10.428'W | 97 | 3 |
| | 67 | Big Bend NP, TX; 29°11.128'N, 103°09.817'W | 87 | 13 |
| | 68 | Big Bend NP, TX; 29°11.169'N, 103°09.927'W | 92 | 8 |
| | 69 | Big Bend NP, TX; 29°09.882'N, 103°00.508'W | 100 | 0 |
| | 70 | Big Bend NP, TX; 29°09.835'N, 103°00.425'W | 99 | 1 |
| 6-3-16 | 71 | Quebradas Byway, NM; 34°03.365'N, 106°46.420'W | 58 | 0 |

curvatures of the longest stems of *Tarantula* plants were almost four times higher than in *V*-form growth forms and reached a high of 28 cm. Fifteen of the 40 stems had both upward and downward stem curvatures. *Tarantula* plants had significantly thinner stems (12.0 ± 0.4 mm) than *V*-form plants (13.5 ± 0.3 mm) (Table 2). Although maximum stem length was longer in *V*-form plants, the number of stems > 50 cm did not differ between growth forms (Table 2).

The 71 transects in which *Tarantula* and *V*-form plants were sampled spanned a distance > 1800 km from Big Bend National Park in Texas to Baja

California, Mexico (Table 1, Fig. 3). In all but three transects, each of which was in the Sierra de las Uvas area of New Mexico, *V*-form plants outnumbered *Tarantula* plants. All transects contained *V*-form plants, but 21 lacked *Tarantula* plants. The mean percentage of *V*-form plants per transect across all 71 transects ($91.1\% \pm 1.7$; range = 23–100%) was higher than that of *Tarantula* plants ($8.9\% \pm 1.7$; range = 0–77%) (t-test, t ratio = 24.8, df = 70, $P < 0.0001$; Fig. 4). Summing all Ocotillos sampled in all transects, 542 of the 6739 (8%) Ocotillos were *Tarantula* growth form plants.

Comparing the six states within the United States and Mexico, only transects in Arizona and New Mexico differed statistically from one another in the percentage of *V*-form plants they supported (ANOVA, F ratio = 3.39, df = 5, $P = 0.0087$; Tukey-Kramer HSD, AZ-NM, $P = 0.0044$; Fig. 5). In Arizona, 99.5% of all Ocotillos sampled per transect were of the *V*-form growth form, yet only 84.4% of Ocotillos were *V*-form plants in New Mexico. More than 90% of all Ocotillos sampled per transect in Baja California, California, Sonora, and Texas were *V*-form plants.

DISCUSSION

The wide distribution and significant abundance of the atypically shaped Ocotillos observed in this study confirm the existence of a previously undescribed, unnamed growth form of Ocotillo. That growth form, termed *Tarantula*, is characterized by having: a) a ratio of <0.8 between the maximum height above ground of its longest stem and the maximum length of the same stem, b) an angle between the longest stem and the ground of <50°, and c) a significant horizontal or downward arching curvature. This whole-plant architecture is distinctly different from the more typical growth form, termed *V*-form, that is characterized by having: a) a ratio of

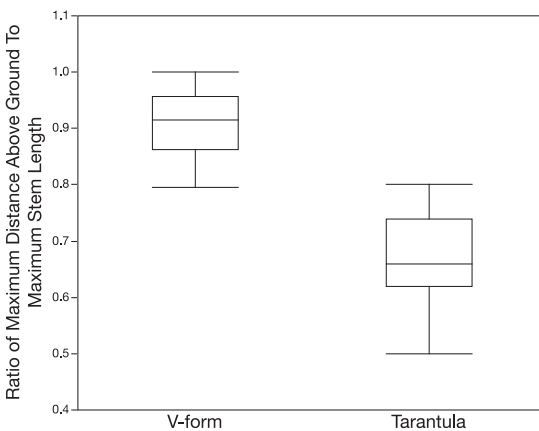


FIG. 2. Mean, median, first and third quartiles, and ranges of the ratio between the maximum height above ground of the longest stem of a plant and the maximum length of the same stem for 32 adjacent pairs of *Tarantula* and *V*-form growth forms of Ocotillo (*Fouquieria splendens*) growing in the foothills of the Organ Mountains in southern New Mexico. Mean ratio for *Tarantula* plants was higher than that for *V*-form plants (t-test, t ratio = -14.38, df = 57, $P < 0.0001$). Mean distance between each pair of plants was 3.9 m. A ratio of 1.0 represents a perfectly vertical stem.

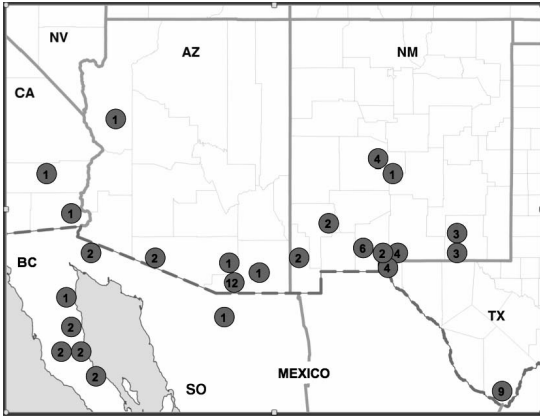


FIG. 3. Locations of the 71 transects in Arizona (AZ, 17), Baja California, Mexico (BC, 9), California (CA, 2), New Mexico (NM, 27), Sonora, Mexico (SO, 3), and Texas (TX, 13) sampled to tally *Tarantula* and *V-form* growth forms of Ocotillo (*Fouquieria splendens*). The number in each dot is the number of transects sampled in that area.

≥ 0.8 between the maximum height above ground of the longest stem of a plant and the maximum length of the same stem, b) angles between the longest stem and the ground of $>50^\circ$, and c) the primarily straight, upright orientation of most stems.

Other than the subspecies and varieties of Ocotillo expertly described by Henrickson (1972), none of which fit the description of *Tarantula* plants, the only reference that specifically mentions "two distinct growth forms" of Ocotillo appears to be Cox and Hunt (1994). In this paper on pocket gopher herbivory in southern California, the authors described a "slender form" and a "stout form" of Ocotillo. However, both forms held erect stems. Additionally, the possibility that *Tarantula* and *V-form* plants could be true subspecies or varieties seems remote, at best, given their observed close proximity to one another and their consistent co-occurrence in mixed populations.

The question still remains as to what causes the atypical architecture of the *Tarantula* plants. Six hypotheses are explored below.

Hypothesis No. 1. *Tarantula* plants are much younger or older than adjacent *V-form* plants. That would not necessarily make a difference in architecture, but very old Ocotillos often have stems that arch over as death nears (Killingbeck unpublished data). None of the Ocotillos scored in this study held senescing stems and the Ocotillos scored to be *Tarantula* plants typically were of similar age to adjacent *V-form* plants as evidenced by the similar number of mature stems, a general proxy for relative age (Darrow 1943). Very young stems initially have soft tissues for a short time but stiffen rapidly and usually do not deviate from an erect posture. Additionally, cohorts of nursery-grown, even-age seedlings from the same seed source have been noted to eventually include a small percentage of *Tarantula*-type plants (Gene Joseph, Plants for the Southwest and Living Stones Nursery personal communication).

Hypothesis No. 2. *Tarantula* plants are the result of extreme differences in soil properties. Even though desert soils can be highly heterogeneous and the soils in New Mexico are particularly varied (Dick-Peddie 1993), pairs of *Tarantula* and *V-form* plants as close together as 0.5 m likely minimize, but do not entirely eliminate, the possibility that soil differences are a causal agent in the formation of the *Tarantula* growth form.

Hypothesis No. 3. *Tarantula* plants are the result of some aspect of herbivory. Observed herbivory on young, emergent stems of Ocotillo by black-tailed jackrabbits (*Lepus californicus* Gray 1837) in north-eastern Sonora, Mexico, has been linked to deviations in overall Ocotillo architecture (P. Dayton, Scripps Institution of Oceanography personal communication). However, the affected plants did not have the low, arching stems characteristic of the *Tarantula* growth form. Other observed herbivory on Ocotillos, such as subterranean feeding by pocket gophers (*Thomomys bottae* [Eyedoux and Gervais 1836]; Cox and Hunt 1994) and consumption of flowers by mule deer (*Odocoileus hemionus* Rafinesque, 1817; Gallina et al. 2017) would seem to have little impact on Ocotillo stem architecture.

Hypothesis No. 4. *Tarantula* plants are the result of having thinner stems. The longest stems of the 20

TABLE 2. SELECTED CHARACTERISTICS OF 20 ADJACENT PAIRS (N = 40) OF *TARANTULA* AND *V-FORM* OCOTILLOS (*FOUQUIERIA SPLENDENS*) IN THE FOOTHILLS OF THE ORGAN MOUNTAINS ON 29 MAY 1998. 'Angle of stem' is the angle from the ground in degrees for the longest stem. Diameter at half-length is the diameter of the longest stem at half its length. Curvature is the maximum departure from straight of downward or upward curves in the longest stem. Mean distance between each pair of plants was 2.9 m. Probabilities of difference between *Tarantula* and *V-form* plants were generated with t-tests.

| Characteristics | <i>Tarantula</i> | <i>V-form</i> | Comparison |
|------------------------------|------------------|----------------|-------------------|
| Angle of stem ($^\circ$) | 37 \pm 1.6 | 66 \pm 1.7 | V > T; P < 0.0001 |
| Max stem length (cm) | 151 \pm 11.5 | 192 \pm 14.5 | V > T; P = 0.033 |
| # Stems > 50 cm | 16.1 \pm 2.0 | 12.4 \pm 1.3 | V = T; P = 0.139 |
| Diameter at half-length (mm) | 12.0 \pm 0.4 | 13.5 \pm 0.3 | V > T; P = 0.002 |
| Curvature downward (cm) | 15.0 \pm 1.6 | 3.9 \pm 0.4 | V < T; P < 0.0001 |
| Curvature upward (cm) | 0.6 \pm 0.4 | 3.5 \pm 0.8 | V > T; P = 0.002 |

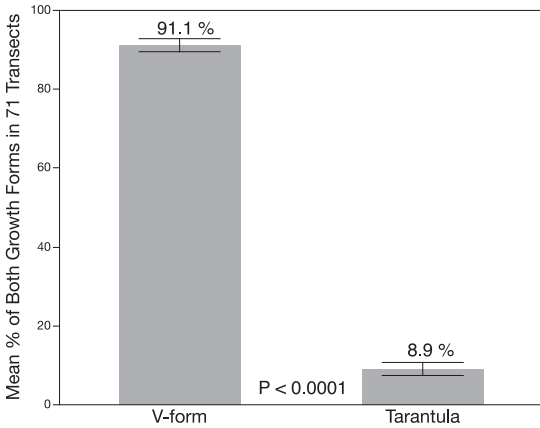


FIG. 4. Mean percentage per transect of *Tarantula* and *V-form* Ocotillos (*Fouquieria splendens*) in 71 transects. The probability of difference between the means is $P < 0.0001$ (t-test, t ratio = 24.8, df = 70). Error bars are standard error of the mean.

Tarantula Ocotillos measured in 1998 did have significantly thinner stems than their adjacent *V-form* plants. If thin stems are weaker, and there is no evidence that they are, or are not, then this hypothesis may have merit. Stiffness tests similar to those used by Niklas et al. (1999) may be useful in the future to test Ocotillo stem strengths. A subspecies of *F. splendens*, *F. splendens* ssp. *campanulate* (Nash) Henrickson, is known to have “much thinner young stems” than *F. splendens* (Henrickson 1972), but its “candelabraform habit consisting of ascending straight branches” (Henrickson 1972; see his Fig. 1c) appears to lack the low, arching stems of *F. splendens*. Even if thinner stems are found to be: a) substantially weaker than thicker stems, b) a consistent feature of *Tarantula* plants, and c) part of the cause for their arching stems, this would still not reveal the cause of stem thickness differences between *Tarantula* and *V-form* plants.

Hypothesis No. 5. *Tarantula* plants are the result of mechanical forces exerted on Ocotillo stems by agents such as wind. In experiments designed to examine the function and distribution of tension wood and gelatinous fibers in Ocotillo stems, DeBevoise (2017) found that these tissues were distributed in such a way as to resist “bending due to gravitational forces and possibly wind.” It is not known whether these tissues differ between *Tarantula* and *V-form* plants, but it is hard to imagine wind alone creating an architecture of stems spread fairly evenly in 360° rather than in a one-sided, krummholz-type arrangement.

Hypothesis No. 6. *Tarantula* plants are the result of hybridization between *F. splendens* and another species of *Fouquieria*. This possibility is unlikely given the large distances between *F. splendens* and the ten other species of *Fouquieria*, all of which have geographical distributions restricted to Mexico (Henrickson 1969). Although hummingbirds, fre-

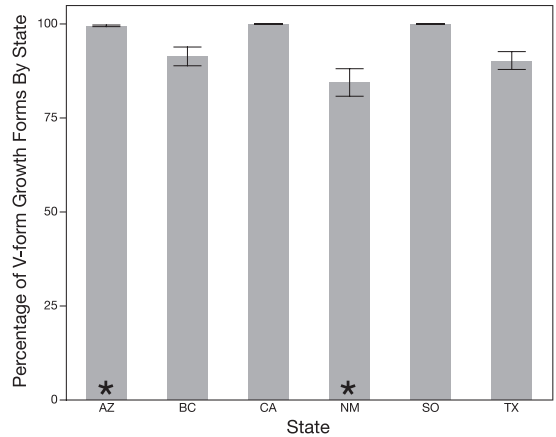


FIG. 5. Mean percentage per transect of *V-form* growth form Ocotillos (*Fouquieria splendens*) in Arizona (AZ), Baja California (BC), California (CA), New Mexico (NM), Sonora (SO), and Texas (TX). The two asterisks identify the only two states in which the percentage of *V-form* Ocotillos differed significantly from one another (ANOVA, F ratio = 3.39, df = 5, $P = 0.0087$; Tukey-Kramer HSD, AZ-NM, $P = 0.0044$). Error bars are standard error of the mean.

quent pollinators of *Fouquieria* (Waser 1979), migrating northward from Mexico could conceivably deliver pollen to *F. splendens* from other species of *Fouquieria* (N. Waser, University of Arizona personal communication), all these species from Mexico have upright stems (Henrickson 1972) and do not resemble *Tarantula* plants.

No definitive explanation is apparent to explain the relatively infrequent, but widespread existence of the *Tarantula* growth form. Future studies to explore causes of the *Tarantula* growth form should include at least one or more of the following: a) DNA analyses to search for potential genetic differences from *V-form* plants, or evidence of hybridization, b) collection and germination of seeds from *Tarantula* plants to discover the architecture of mature specimens, and c) removal of the inner stems of very young *V-form* plants to mimic early-age herbivory and determine whether such action gives rise to the *Tarantula* growth form.

While descriptions of Ocotillo’s V-form shape and Cornett’s (2017) observation of “Ocotillo’s splendid uniformity of form” still hold for more than 90% of individuals of this intriguing species, a significant fraction of Ocotillos take on an unmistakably different, previously undescribed growth form. Whatever the reason for its existence, the *Tarantula* growth form of Ocotillo is a visually distinct, widely distributed variant of *Fouquieria splendens* that merits further study.

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LITERATURE CITED

- BENSON, L. AND R. A. DARROW. 1944. A manual of southwestern desert trees and shrubs. University of Arizona Biological Bulletin No. 6, Tucson, AZ.
- CORNETT, J. W. 2017. The splendid Ocotillo. Nature Trails Press, Palm Springs, CA.
- COX, G. W. AND J. HUNT. 1994. Pocket gopher herbivory and mortality of Ocotillo on stream terrace, bajada, and hillside sites in the Colorado Desert, southern California. *Southwestern Naturalist* 39:364–370.
- DARROW, R. A. 1943. Vegetative and floral growth of *Fouquieria splendens*. *Ecology* 24:310–322.
- DEBEVOISE, D. M. 2017. Functions of gelatinous fibers in the roots and shoots of *Fouquieria splendens*. Unpublished M.S. thesis, California State Polytechnic University, Pomona, CA.
- DICK-PEDDIE, W. A. 1993. New Mexico vegetation: past, present, and future. University of New Mexico Press, Albuquerque, NM.
- GALLINA, S., L. G. FERIA, AND R. GONZÁLEZ-TRÁPAGA. 2017. Ocotillo flowers as food resource for the mule deer during the dry season. *Therya* 8:185–188.
- HENRICKSON, J. 1969. An introduction to the Fouquieriaceae. *Cactus and Succulent Journal* 41:97–105.
- . 1972. A taxonomic revision of the Fouquieriaceae. *Aliso* 7:439–537.
- KILLINGBECK, K. T. 2019. Stem succulence controls flower and fruit production but not stem growth in the desert shrub Ocotillo (*Fouquieria splendens*). *American Journal of Botany* 106:223–230.
- NIKLAS, K. J., F. MOLINA-FREANER, AND C. TINOCO-OJANGUREN. 1999. Biomechanics of the columnar cactus *Pachycereus pringlei*. *American Journal of Botany* 86:767–775.
- SHREVE, F. 1917. The establishment of desert perennials. *Journal of Ecology* 5:210–216.
- TURNER, R. M., J. E. BOWERS, AND T. L. BURGESS. 1995. Sonoran Desert plants: an ecological atlas. University of Arizona Press, Tucson, AZ.
- WASER, N. M. 1979. Pollinator availability as a determinant of flowering time in Ocotillo (*Fouquieria splendens*). *Oecologia* 39:107–121.