

Morphology and mechanical properties of junctions: Implications on the success of clonal spread of cacti



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ABSTRACT

Opuntoid cacti reproduce asexually through separation and subsequent rooting of stems (cladodes in platyopuntias; joints in cylindropuntias). Consequently, the force that keeps them together must be overcome. This work assesses the morphometry and disjunction force of joints in *Tephrocactus aoracanthus*. Morphologically, during their maturation, joints change in shape from oval to spherical, resulting in the youngest being significantly shorter and lighter than the oldest ones. Both critical bending moment and section modulus of junctions resulted in weaker connections on younger joints with respect to older ones, determining that young joints can be separated with less force applied. According to that, their deflection angle is smaller compared to older joints. In relation to other species, the junction of *T. aoracanthus* is more fragile in both the youngest and oldest joints. This mechanism could favor the spread of *T. aoracanthus* and its colonization of sites unfavorable for the establishment of its seedlings.

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1. Introduction

In extremely arid environments, plant species that reproduce both sexually (seeds) and asexually (cladodes or joints) have certain advantages over those reproducing only through the sexual route because the elements of asexual origin are usually made up of mature tissues, which enables them to colonize unfavorable environments for seeds and seedlings that often need the nurse effect of other plants (Méndez et al., 2004; Clark-Tapia et al., 2005; López and Valdivia, 2007; Almirón and Martínez Carretero, 2010, 2015). Most opuntoid cacti can generate new individuals from the separation and rooting of stems developed from axillary buds on older stems (Mauseth, 2006). Each stem has significant reserves of water and photosynthates, plus the ability to produce adventitious roots in order to form a new individual, but without contributing to the genetic diversity of the population (Mandujano-Sánchez, 2007). In this sense, some authors suggest that the clonal reproduction of some opuntoid cacti is a key component in maintaining population

stability, it sometimes being more important than sexual reproduction (Clark Tapia et al., 2005; Mandujano et al., 2007).

The separation of stems occurs when the mechanical strength is overcome by some external force. In some cases, the weight of the branch may be sufficient, while in others application of an external force is necessary. Bobich and Nobel (2001) showed that the minimum force necessary to separate the cladodes of *Opuntia ficus-indica*, *Opuntia littoralis* and their hybrid (*Opuntia occidentalis*) is related to the bonding area of cladodes and their different types and proportions of vascular elements in this area. Since the cladode junctions in *O. occidentalis* were much weaker than in the other species studied, these authors suggest that, because of its clonal reproduction, the hybrid has greater ability to recover its population after environmental disturbances.

Tephrocactus aoracanthus (Lem.) Lem. is a cylindropuntia distributed in the central-west of Argentina, principally on gentle hillsides or stony/sandy plains between 500 and 2500 m in altitude where it is the dominant cactus (Kiesling, 1984). This species forms high-density populations, with individuals grouped in clusters from 0 to 1 m in diameter, generally independent of surrounding shrubs (Almirón and Martínez Carretero, 2013a). The branches that reach 50 cm in height are made up of spherical joints aligned. Some

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aspects of the reproductive biology of *T. aoracanthus* were studied, such as joint rooting and seed germination. In laboratory assays, 95% of the analyzed joints developed adventitious roots. However, only those joints placed in sandy substrate rooted successfully, while the adventitious roots of joints placed in rocky substrate never penetrated the soil deeply. On the other hand, in laboratory assays under controlled light and temperature conditions the rates of germination was always lower than 8% (Almirón and Martínez Carretero, 2013b).

This evidence would indicate an important incidence of agamic reproduction on population maintenance, like in other opuntoid cacti (Mandujano et al., 2007).

Because joint failure is the first step by which new ramets are available for agamic spread, this experimental study is relevant. We expect that joint failure would be related to both the inherent characteristics of the junction area and the magnitude of applied forces.

The objective of this study was to assess joint morphology and the biomechanical properties of junctions in *T. aoracanthus*. The results obtained, linked to previous spatial distribution analysis (Méndez et al., 2004; Almirón and Martínez Carretero, 2013a), would explain the role of clonal reproduction in the spread of this species, as mentioned in several reports (Kiesling, 1984; Méndez et al., 2004; Almirón and Martínez Carretero, 2013b) in these hyper-arid environments.

2. Materials and methods

2.1. Study area

The material for this study was collected from the Matagusanos Valley (31° 13' 17" S–68° 39' 7" W) in San Juan province, Argentina. Mean annual temperature is 16 °C (absolute maximum and minimum temperatures are 42.8 and –7.3 °C, respectively). Annual precipitation is 100 mm, 70% occurring in the summer period (Le Houérou et al., 2006; Abraham et al., 2009), which can produce runoff with large amounts of transported material (heterodiametric clasts and parts of plants). Floristically, the landscape is dominated by shrubs like *Bulnesia retama* (Gillies ex Hook. & Arn.) Griseb., *Larrea divaricata* Cav. and *Cercidium praecox* (Ruiz & Pav.) Burkart & Carter, among others. Average plant cover is 20%.

2.2. Experimental design

Thirty mature branches of *T. aoracanthus* were randomly collected in the field. Each branch consisted of three joints vertically aligned and labeled 1st, 2nd and 3rd, from the branch top downward. The junctions were called “terminal” (between 1st and 2nd joints) and “sub-terminal” (between 2nd and 3rd joints). The biomechanics of junctions was studied using the technique proposed by Nobel and Meyer (1991) with some modifications according to the characteristics of *T. aoracanthus*. First, the 2nd joint of each branch was fastened to a rigid scaffold with wooden clamps and with inextensible cords attached to four screws fixed on the scaffold. Forces were applied to the upper joint using a steel wire attached to a screw placed in coincidence with the center of the joint and secured with nuts and washers. The steel wire passed over a low-friction pulley adjusted so that the applied forces were always perpendicular to the upper joint face. Angular deflections were read directly on a semicircular angle degree scale mounted above the upper joint, which had a fine steel needle inserted into its apex the angle degree scale replaced that with millimeter gradations originally used in Nobel and Meyer (1991) in order to directly obtain measures of angular deflection. The gradient of applied mass was standardized at 100-g mass intervals, determining the

variation of angular deflection in relation to increase in applied mass, until junction failure. After that, the 3rd joint was fixed to the scaffold and the forces were applied to the 2nd joint, repeating the experiment for the sub-terminal junction. Next, height, maximum diameter of each joint and diameter of junctions were measured with a Vernier caliper and joint weight with a digital balance (5000 ± 1 g). To prevent possible effects of dehydration on joints, all tests were performed in the field, immediately after collecting the joints. All these variables were compared with analysis of variance, and mean separation with Tukey test ($\alpha < 0.05$).

In all three joint categories, linear regressions were calculated between height and diameter in order to know their geometric relationship. The bending moment (Nm) was calculated by multiplying the force applied (applied mass by gravitational constant) by the moment arm (0.5 × joint length). The section modulus (I/a), which is the geometric component that describes resistance to the bending moment (Niklas, 1992), was calculated from the semi-minor axis (a) of the junction area, using the following equation: $I/a = \pi a^3/4$, where I is the second moment of area.

Volumes of both the joints (1st, 2nd and 3rd) and the junction areas (terminal and sub-terminal) were obtained with ovoid volumetric and circular area equations, respectively.

3. Results

Diameter, height, weight and volume of the 1st joint were significantly lower versus the 2nd and 3rd joints (Table 1). The linear regression between height and diameter (in each joint category) was significant ($p < 0.005$, all with 1 degree of freedom): 1st joint: $R^2 = 0.25$ ($F = 9.32$); 2nd joint: $R^2 = 0.47$ ($F = 24.41$), and 3rd joint: $R^2 = 0.53$ ($F = 30.24$). The slope of regression curve in the 1st joint ($y = 0.81x + 0.99$) indicated a diameter larger than height, while slope of the 2nd and 3rd joints ($y = 1.07x - 0.43$ and $y = 1.09x - 0.61$, respectively) was close to 1, indicating spherical geometry.

The Tukey test ($p < 0.0001$; $F = 75.29$) showed that the terminal junction area was significantly smaller than the sub-terminal one ($0.63 \text{ cm}^2 \pm 0.32 \text{ SD}$ and $1.60 \text{ cm}^2 \pm 0.54 \text{ SD}$ respectively; both with 1 degree of freedom). Hereby, failure of the terminal junction always occurred with less mass applied (breaking mass) than required by the sub-terminal junction (Fig. 1a). Linear regressions between junction areas and breaking mass were significant for both terminal ($y = 1.02x + 0.51$; $R^2 = 0.24$; $p < 0.0068$; $F = 8.58$) and sub-terminal junctions ($y = 0.79x + 0.88$; $R^2 = 0.19$; $p < 0.0164$; $F = 6.56$), both with 1 degree of freedom. The critical bending moment and section modulus were always smaller in the terminal than the sub-terminal junction (Fig. 1b). The linear response of the deflection angle to the increase in applied mass was similar between terminal and sub-terminal junctions, although the mean of breaking mass was significantly lower ($p < 0.0001$; $F = 23.08$) for the terminal compared to the sub-terminal junction (1.16 kg and 2.19 kg, respectively) (Fig. 2).

4. Discussion

Considering that the joints of *T. aoracanthus* are discrete annual growth units and that the branches analyzed consisted of three aligned joints, it is evident that joints change from ovoid to spherical, stopping their growth in shape, volume and weight as of the second year of development. Anyway, joints developed in one year are potentially suitable for clonal spread (Almirón and Martínez Carretero, 2013b).

The relationship between terminal/sub-terminal junction areas indicates important differences between *T. aoracanthus* (0.39) and the species analyzed by Bobich and Nobel (2001): *O. ficus-indica*

Table 1
Analysis of variance and mean separation (Tukey test), between morphometric parameters of all joints categories. Different letters shows significant differences ($\alpha < 0.05$). In parenthesis, standard deviation.

Cladode	Diameter (cm)	Height (cm)	Weight (g)	Volume (cm ³)
	F: 25.16; p < 0.0001	F: 11.16; p < 0.0001	F: 32.99; p < 0.0001	F: 18.42; p < 0.0001
1st	5.30(0.48) a	5.28(0.78) a	81.47(18.15) a	79.11(21.52) a
2nd	6.10(0.45) b	6.11(0.71) b	127.33(27.40) b	120.98(28.85) b
3rd	6.25(0.71) b	6.26(1.07) b	135.77(35.35) b	133.44(51.61) b

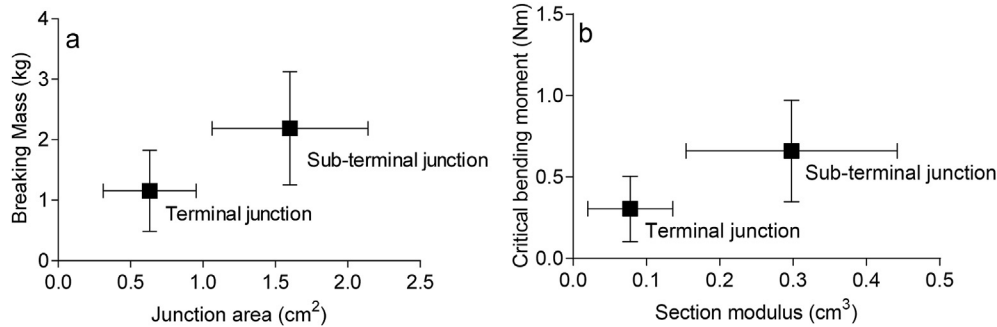


Fig. 1. Relationship between (a) the breaking masses and the mean junction area and (b) the critical bending moment and the section modulus for terminal and sub-terminal junctions of *T. aoracanthus*. Data are means \pm standard deviation for both independent and dependent variables ($N = 30$ branches).

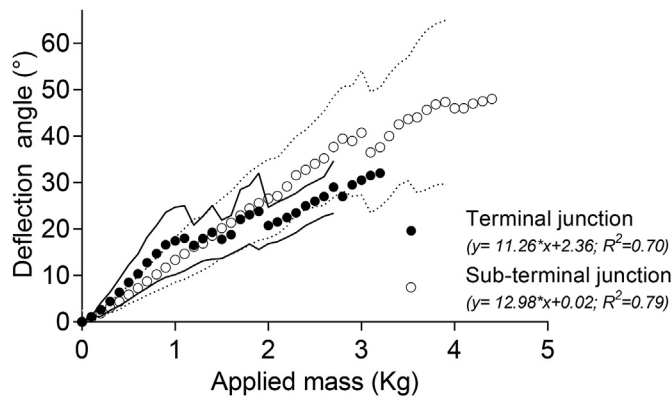


Fig. 2. Effects of applied forces on the angular deflection for terminal and sub terminal junctions of *T. aoracanthus*. Both, black (terminal) and white (sub-terminal) points are average values of deflection angle for each applied mass value. Solid and dotted lines, represents standard deviation from lineal regression in terminal and sub terminal junctions respectively. ($N = 30$ branches).

(0.71); *O. litoralis* (0.53) and *O. occidentalis* (0.59). Application of a lateral force to the top end of an entire branch in any of these species is expected to cause the first joint to separate from the branch, and the second joint to remain on the plant, avoiding its complete destruction. Anyway, according to the proportions observed, junctions of *T. aoracanthus* are weaker than junctions reported for platyopuntias by Bobich and Nobel (2001).

The low mechanical resistance observed between joints of *T. aoracanthus* (chiefly in the terminal junction) linked to early adventitious root emergence (Almirón and Martínez Carretero, 2013b) would indicate that agamic replication is a successful mechanism used by this cactus.

In normal plant development, it is expected that increase in the number of joints in the same branch could produce its spontaneous failure, due to forces produced by the sum of the weight of all joints. Later, secondary transport by runoff of joints and their rooting occurs successfully (Almirón and Martínez Carretero, 2013b), so a

spatial distribution in dense clusters is expected, as was observed by Almirón and Martínez Carretero (2013a), with a similar pattern to that of other opuntoid species (Carrillo-Ángeles and Mandujano, 2011). Future studies analyzing populations from a genetic perspective will elucidate how this dispersal process affects population diversity and stability (Carrillo-Ángeles et al., 2011).

The results obtained here point to the importance of executing trials in order to assess the role of the different biotic and abiotic factors present in each environment, which are capable of reaching the minimum force required to separate and transport joints.

Particularly in the study area, there are signs that intense runoff produced by summer rains can separate and transport joints of *T. aoracanthus*, a hypothesis that we are now testing empirically.

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