



Canopy architecture and PAR absorption of *Euphorbia cooperi* in the Matobo Hills, Zimbabwe

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ABSTRACT

Tree euphorbias share many traits with arborescent cacti in having tall and multi-branched forms of growth which have selective value for maximizing photosynthetic surface area and water storage. The candelabra growth form of *Euphorbia cooperi*, and likely other *Euphorbia* species with similar canopy architecture in southern Africa, allows these plants to add photosynthetic surface area as they grow and increase in size while at the same time minimizing problems of transpirational water loss. This increase in branch surface area occurs with age and increase in size and numbers of branches at the same time that the amount of potential storage volume to support water loss from this expanded surface area is also increasing. Key to this ability is the morphological trait of a heavily suberized trunk that increases with age, providing added capacity for water storage without adding to surface area subject to transpirational water loss. This trait and the associated canopy architecture allows the development of increasing surface area with minimal self-shading as new branches develop so long as older branches are shed. Beyond the canopy architecture, the cross-sectional morphology of branches in *E. cooperi* with concave faces has selective value in balancing increased surface area with maintenance of adequate storage volume. Simulated patterns of branch morphology with a square cross-sectional morphology show a “safe” result in producing little change in S:V ratio as plants mature, but at the expense of limiting photosynthetic surface area. At the other extreme, a simulated cross-sectional morphology with deep concave flutes, as seen in young plants, would significantly increase photosynthetic surface area, but at a potential cost of increased sensitivity to drought stress.

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1. Introduction

Much has been written about the growth form of arborescent cacti in the Southwestern United States and Mexico, with a particular emphasis on the significance of branching architecture on photosynthesis, water storage and its conservation, and reproductive success (Yeaton et al., 1980; Cody, 1984; Geller and Nobel, 1986, 1987; Drezner, 2003). In comparison, there has been little speculation about the significance of morphological variation in branching structure and architecture of tree euphorbias in southern and eastern Africa and Madagascar. Here, a diverse set of arborescent euphorbias occurs with a wide range of distribution across southern and eastern Africa and extending to the Arabian Peninsula and across the continent to Southeast Asia (White et al., 1941). Such growth forms and the associated succulence with crassulacean acid metabolism (CAM) have evolved multiple times within the genus and stimulated diversification in these lineages (Bruyns et al., 2011; Evans et al., 2014; Horn et al., 2014).

Tree euphorbias present an interesting group for study because of the diversity of forms in canopy architecture which they include.

Several species of tall tree euphorbias, as with *Euphorbia ingens* and *E. grandidentata*, have a broad primary trunk and long-lived secondary branches that are maintained on the lower trunk to form a broad, rounded canopy. More common, however, are tree euphorbias with a candelabra-shaped crown of multiple succulent branches. This crown shape results as older branches are shed with age. The candelabra growth form has evolved multiple times and includes at least six species in northeastern South Africa (*E. confinalis*, *E. cooperi*, *E. evansii*, *E. excelsa*, *E. sekhukhuniensis*, *E. triangularis*, and *E. sp. A.*; Schmidt et al., 2002).

We report on a field study of the morphology and branching architecture in *Euphorbia cooperi*, a widespread tree euphorbia that exemplifies a candelabra form of canopy architecture. We explore how branching form, architecture and associated surface to volume ratio of branches can impact the ecology and/or ecophysiology of this species. What is the tradeoff between a few broad branches in contrast to more numerous smaller diameter branches that characterize *E. cooperi*? In addition, what is the significance of branch cross-sectional shape? An increase in branch perimeter ratio, i.e. the ratio of cross-sectional perimeter to diameter, will increase the ratio of photosynthetic surface area (S) to plant volume (V). Such an increase in S:V ratio would increase whole plant CO₂ uptake assuming that branches are arrayed architecturally to minimize self-shading. In contrast, growth forms with a lower S:V ratio can store a larger

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volume of water, and utilize this water to extend the growing season. Through simulations of two hypothetical variants in branch perimeter ratio, we examine the consequences of cross-sectional shape on photosynthetic surface area and volume available for water storage. In our discussion we compare and contrast our results with what is known about the morpho-physiology of canopy architecture in arborescent cacti.

2. Materials and methods

2.1. Study species

Euphorbia cooperi is a tall, multi-branched, arborescent tree euphorbia that reaches heights of 10 m or more. It occurs across a range of soil and vegetation types, most typically on rocky outcrops and ridges. It is also geographically widespread with a distribution ranging from KwaZulu-Natal, Swaziland, North-West Province, Mpumalanga and Limpopo in South Africa to Mozambique, Zimbabwe and Botswana, Zambia, and Tanzania.

The canopy architecture of *E. cooperi* includes large numbers of branches at the upper section of the trunk, giving it a rounded crown (Fig. 1A). The cross-sectional morphology of the branches in our population was largely 4-sided with moderately fluted ridges along each of the margins, but branches are often 5-sided in other populations. The old branches on the lower and middle trunk are shed with age, while the outer margin of crown branches curves upward as they develop, giving the tree a candelabra appearance and hence the common name candelabra euphorbia. The trunk of *E. cooperi* is subject to weathering and sun damage (Evans and Abela, 2011; Evans and Scelsa, 2014) and is not functional for photosynthesis.

The branches of *E. cooperi* have distinct segments along their length, averaging about 12 cm in maximum width and 15 cm in length. Each segment prominently possesses 4 to 6 winged ridges. The segments have an unusual shape that has been described as an inverted heart with the widest section near the base of the segment that tapers to its apical part (Fig. 1B; Gildenhuis, 2006). The spine shields of *E. cooperi* form a continuous horny margin along the angles of the branches with paired spines varying from about 4–10 mm in length. There may also be a pair of minute prickles present above the main spines. Along the spine ridge, the scars of the small rudimentary leaves may also be seen. The inflorescences are formed above the spines on the apical section of each branch (Gildenhuis, 2006). There are three named varieties of *E. cooperi*, with our field work carried out on *E. cooperi* var. *cooperi*.

2.2. Field sampling

Field studies were carried out at Beaconsfield Farm in the Matobo Hills of western Zimbabwe, about 50 km southwest of Bulawayo (lat. 20°38'39.45", long. 28°10'58.37") at 1199 m elevation. The landscape of this uplifted area, termed the Matobos Batholith, is a portion of the ancient granite shield of Zimbabwe and northern South Africa. The differing composition of the granite has produced weathering of the hills into rounded koppies and steep-sided domes with diverse shapes. Fracture zones in the rock allow access of many trees to perched water tables. Runoff from the hills collects in valleys forming local areas of wetlands termed dambos. *Euphorbia cooperi* favors rocky slopes with little or no tree cover, but can also be found on flats in open deciduous woodland. Associated species include *Euphorbia confinalis*, *Euphorbia griseola*, *Combretum imberbe*, *Commiphora marlothii*, and *Ficus thonningii*.

The Matobo Hills are characterized by warm rainy summers and cool dry winters. Mean annual precipitation near the study site at Matobo National Park is 587 mm, with the rainy season extending from November into May during which 87% of the mean annual precipitation takes place (WordClim data – Hijmans et al., 2005). Little or no significant rainfall occurs from May through September. Rainy season mean maximum high temperatures peak at 29–30 °C in October and

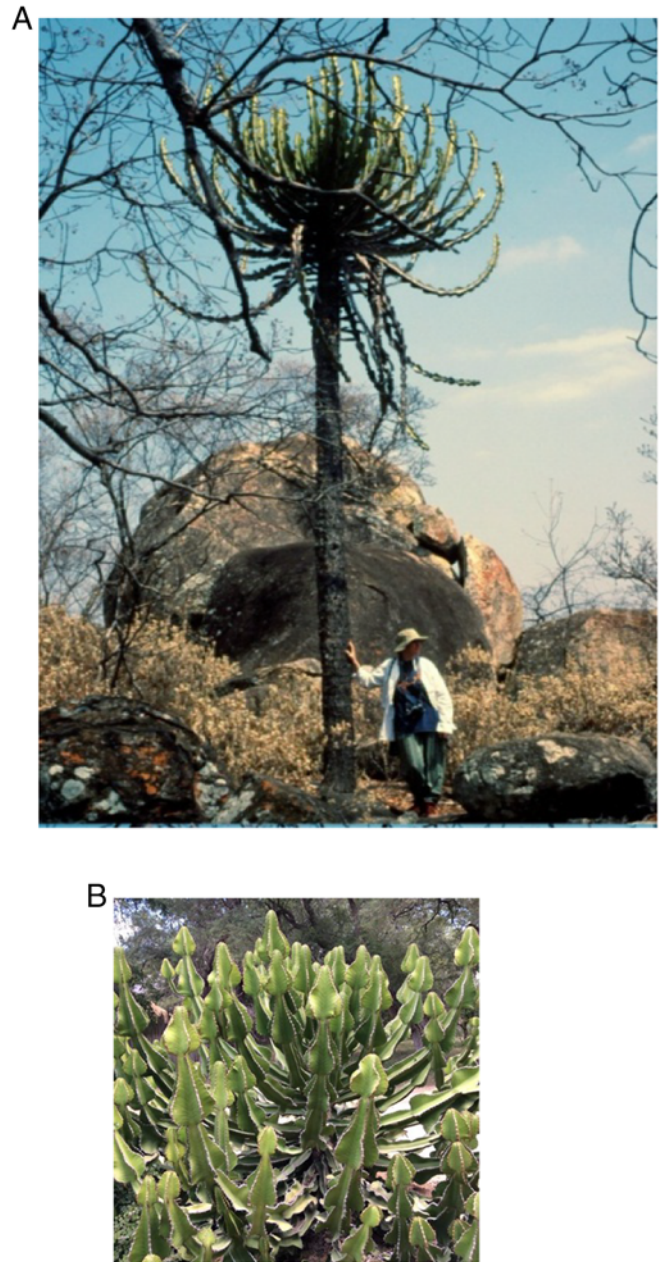


Fig. 1. *Euphorbia cooperi*: 1A. tall tree at Beaconsfield Farm, Matopo Hills; 1B. Young plant showing highly fluted branch segments. Photos P. Rundel.

November, with mean minimum temperature of 14–15 °C in these months. Winter temperatures are cooler with mean maximum temperatures of 21 °C during the day but dropping to 4 °C at night.

Field measurements were made on 133 individuals of *E. cooperi* that included all plants of this species within the study area. Because of the candelabra-form of growth, it was difficult to accurately measure total plant heights. Instead we measured height to lowest branching and basal diameter as analogues for plant size. We estimated that the branching canopy would add 3–4 m to the total height of the largest mature individuals. For each individual, measurements were also made of the number of living branches and mean number of segments per branch. Using a mean value for segment length, segment surface area, and segment volume, calculations were made for each individual of total branch length, total surface area of branches, total volume of branches, volume of trunk below the point of branching, and surface area to volume ratio of branches.

For our field plants, which typically exhibited a branch morphology with four fluted sides, we estimated a mean perimeter to area ratio of $5.5 \text{ m}^2 \text{ m}^{-3}$. In order to examine the significance of branch cross-sectional morphology with winged ridges along each segment, we simulated two alternate branch cross-sectional forms that differed in perimeter to area ratio of branch segments (Fig. 2). One of these was a square stem of the same diameter and a perimeter to area ratio of $4.0 \text{ m}^2 \text{ m}^{-3}$. The other was a stem cross-section with a deeper angular fluting such that the stem core was only 4 cm in diameter, with a resulting perimeter to area ratio of $8.0 \text{ m}^2 \text{ m}^{-3}$. Our simulations used the morphological base data for our sampled population of *E. cooperi*, but substituting these hypothetical perimeters to area ratios in our calculations for surface areas and volumes of the total canopy.

The morphological characteristic of tree diameter was distributed normally within the sample population. Statistical analyses using regression were carried out to test for significant relationships between morphometric measurements described above. Linear regressions provided the best fit for these data.

3. Results

Height to branching in the sampled population of *Euphorbia cooperi* ranged from 1 m to 8.5 m, with a mean height of 3.9 m. Mean basal diameter was 14.6 cm, but ranged as high as 25.4 cm. Height of branching scaled linearly with diameter (Fig. 3). Our measurement was height of branching point, and we estimate that our tallest individual was about 11 m in height, slightly taller than heights previously mentioned in the literature (Schmidt et al., 2002; Gildenhuys, 2006). Branch numbers ranged from less than 5 in the smallest plants sampled to a maximum of 78, with a mean branch number of 34. Branch number also scaled in a linear manner with height of branching (Fig. 4). The number of segments per branch ranged from less than 2 in the small individuals sampled to 28, with a mean of 15.4. These values scaled linearly with height as older plants maintained more segments per branch than smaller plants (Fig. 5).

Although the trunk of *Euphorbia cooperi* is not functional for photosynthesis, the total area of photosynthetic surface is nevertheless very high because of the large number of branches. All branch units are modular structures with very similar diameters and cross-sectional architecture. Thus, a net increase in branch number increases the photosynthetic surface area of a plant, and canopy surface area is linearly related to branching height (Fig. 6). The largest individual in our sample population had 120 m of branch length with 43.5 m^2 of photosynthetic surface area.

The ratio of branch surface area (S) to plant volume including the trunk below the point of first branching (V) showed a significant negative linear relationship with tree height. This $S:V$ ratio averaged about $70 \text{ m}^2 \text{ m}^{-3}$ in small individuals but dropped to about $50 \text{ m}^2 \text{ m}^{-3}$ in the large trees (Fig. 7). Thus, as individuals get larger and add branches to increase photosynthetic surface area, they are at the same time

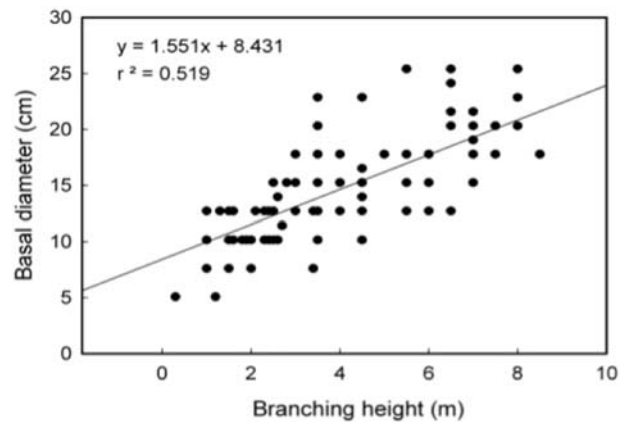


Fig. 3. Morphometric relationships of canopy architecture in *Euphorbia cooperi*. Basal diameter in relation to branching height.

increasing the relative amount of potential storage volume to support water loss from this expanded surface area. This result is made possible because the ratio of branch volume to total volume including the lower trunk also declines linearly with growth as the size of trees increase (Fig. 8), that is to say that the proportion of total storage volume in the trunk increases as the trees grow taller, providing more of a buffer for water loss as photosynthetic surface area increases with the addition of more branch structure.

Our demographic base data allowed us to model two hypothetical differences in branch morphology with changes in branch perimeter ratio, i.e. branch perimeter to cross-sectional area ratio. The cross-sectional morphology of branch segments has an important impact on the ratios of surface area to volume as plants increase in size. With a square cross-sectional shape of the branch segments, the relationship of $S:V$ ratio to branching height has a very flat slope, indicating very little change in storage volume with increasing age (Fig. 9). With this morphology the $S:V$ ratio would be only $30\text{--}40 \text{ m}^2 \text{ m}^{-3}$, providing strong buffering against water loss, but with little or no proportional gain in photosynthetic surface area. At the other extreme, if the cross-sectional form was deeply fluted, the relationship between surface to volume ratio and height would show a steeper slope from ratios of about $120 \text{ m}^2 \text{ m}^{-3}$ in small plants to about $70 \text{ m}^2 \text{ m}^{-3}$ in large individuals, providing much more surface area per unit of stem volume than in the natural stem morphology (Fig. 9).

In contrast, the cross-sectional morphology of branch segments has only a very small impact on the ratio of branch volume to total storage volume including the trunk up to the point of branching. A square cross-sectional morphology with the same diameter would provide a limited increase in this ratio, while a deeply-fluted four-sided branch cross-section would reduce this ratio. The slope of these three cross-

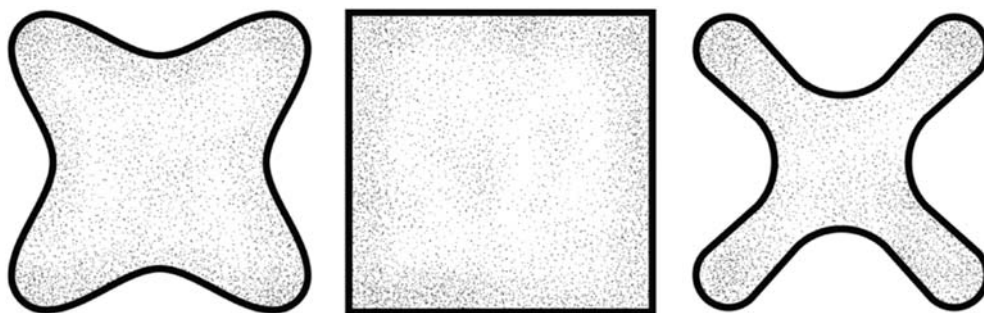


Fig. 2. Modeled step cross-sectional shapes. Mature field plants with a perimeter to area ratio of 5.5; hypothetical square stem with a perimeter to area ratio of 4.0; and hypothetical fluted stem with a perimeter to area ratio of 8.0.

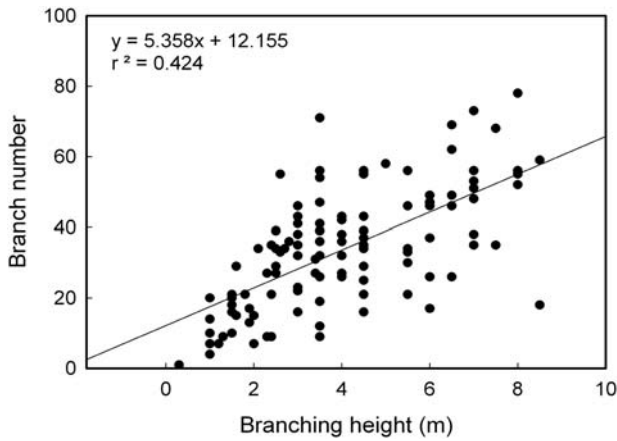


Fig. 4. Morphometric relationships of canopy architecture in *Euphorbia cooperi*. Branch number in relation to branching height.

sectional branch morphologies modeled for our field samples are not significantly different (Fig. 10).

4. Discussion

Multiple stems, branching, and ribbed outer surfaces are common morphological features of shrubby and arborescent cacti. Several functional roles for these traits were hypothesized a century ago including increased stem support, accordion-like flexibility in seasonal changes in water storage, and expanded area surface area for heat dissipation in the desert (Spalding, 1905; MacDougal and Spalding, 1910). More recently, structural engineers have taken an interest in the strength of branching structures of columnar cacti and arborescent monocots with their outer shape of the connection between shoot and branch as well as of the arrangement of the lignified vascular tissues in the branching region. These structures, which are also present in arborescent euphorbias, may be relevant to engineers seeking to design braided fiber-reinforced composites that minimize demand on available design space (Schwager et al., 2010; Masselter et al., 2013).

Like many cacti, arborescent species of *Euphorbia* exhibit a variety of canopy architectures and large surface to volume ratios of their branches. However, a notable difference comes with their woody anatomy and relatively inflexible cross-sectional shape compared to cacti. Tree euphorbias have not been shown to significantly change in cross-sectional volume with water storage. Unlike arborescent cacti whose branches are typically round in cross-section, tree euphorbias display a diversity of cross-sectional morphologies from triangular to

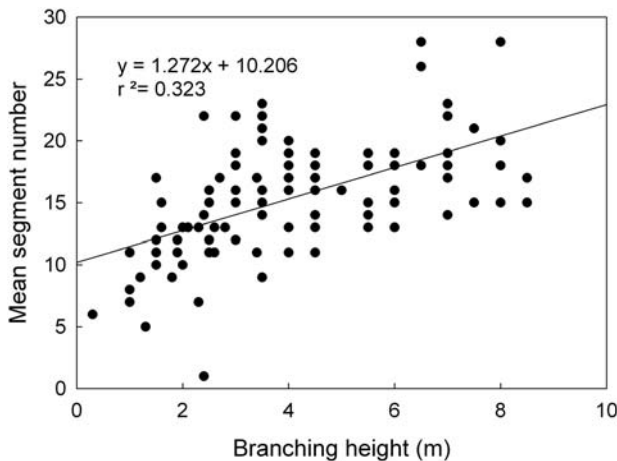


Fig. 5. Morphometric relationships of canopy architecture in *Euphorbia cooperi*. Mean segment number in relation to height of branching

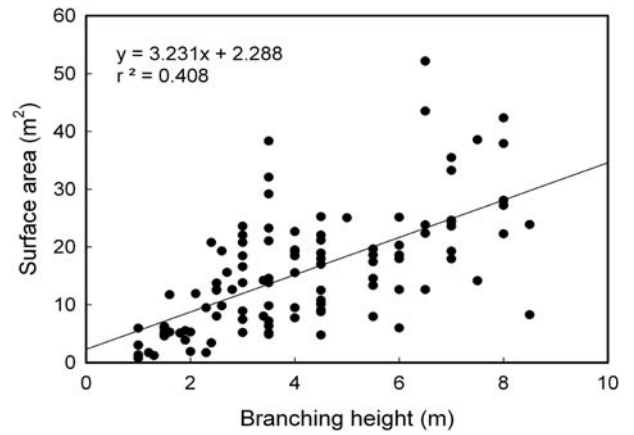


Fig. 6. Morphometric relationships of canopy architecture in *Euphorbia cooperi*. Branch surface area in relation to branching height. All graphs have a significant linear relationship with $p < 0.001$.

square and four sided, and even 5 to 6-sided branch morphologies with deep angular flutes (White et al., 1941).

Recent studies have strongly suggested that stem and branch surface architecture in arboreal succulents is strongly influenced by strategies of maximizing the interception of photosynthetically active radiation (PAR) (Nobel, 1981; Geller and Nobel, 1986, 1987). While it may not seem intuitive to think that tall stem succulents growing in open high-light environments would be light-limited, morphological designs in cacti that increase PAR interception have been shown to increase net carbon uptake. These same principles of morphological form and function apply to succulent euphorbias.

An increase in branch perimeter ratio, as with deeply fluted wings in the cross-sectional morphology, acts to increase the ratio of surface area to plant volume, raising whole plant CO₂ uptake. A lower S:V ratio, assuming constant cuticular conductance, would reduce water loss and allow the potential for continued growth during extended drought. Studies with the multi-stemmed cactus *Stenocereus thurberi* have shown that with an S:V ratio of 31 m² m⁻³, this species has a S:V value 3.8 times higher than an unbranched plant of the same volume (Geller and Nobel, 1986). The large amount of branching in *Euphorbia cooperi* allows these plants to maintain a higher S:V ratio from about 70 m² m⁻³ in small plants to 50 m² m⁻³ in mature individuals. The pattern of highest S:V ratio in young plants may have selective value in promoting successful establishment.

A multi-stemmed architectural design in tree euphorbias has an important impact on PAR interception and thus CO₂ uptake. Increasing branch number in *Euphorbia cooperi* with age provides a steady increase in total PAR interception as long as the branches are arranged to prevent

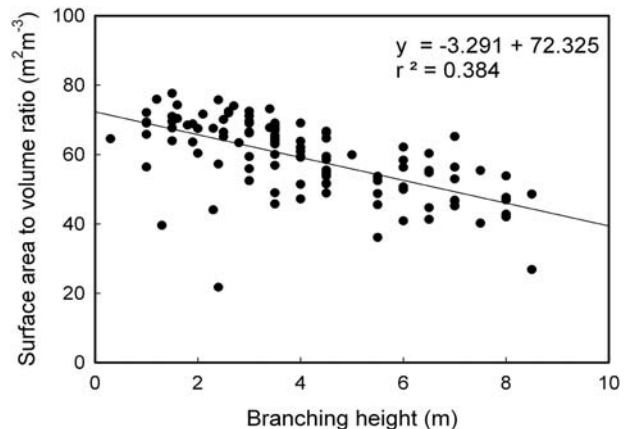


Fig. 7. Surface area to volume ratio for branches of *Euphorbia cooperi*.

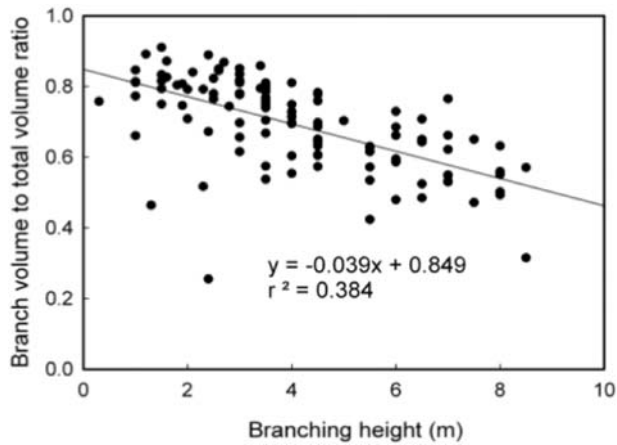


Fig. 8. Relationship of branch volume to total volume including the basal trunk in *Euphorbia cooperi*. Graphs have a significant linear relationship with $p < 0.001$.

excessive self-shading. Like many other tree euphorbias, older branches of *E. cooperi* are shed with age. Because segments appear to represent nodes of annual growth (see Cowling et al., 2010), results from our samples suggest that the mean age of branches is 15 years, and that larger individuals can keep their branches alive for as long as 28 years before dehiscence. The median length of these segments at 15 cm is comparable to that of annual growth segments marked by waxy bands in *Lemaireocereus aragonii*, a Costa Rican arborescent cactus (Buskirk and Otis, 1994).

Is self-shading an issue for larger individuals of *Euphorbia cooperi* where there may be as many as 80 or more branches? The impact of self-shading can sometimes be seen in the field in individual plants of *Euphorbia cooperi* where there exists a particularly dense canopy of branches. Fig. 11 shows such an example in Kruger National Park with major dieback visible on older segments of an otherwise photosynthetically active canopy. While we cannot absolutely eliminate frost as a cause of this pictured dieback, freezing damage would be expected to be most apparent on young branch tissues exposed in the upper canopy.

The impact of self-shading in multi-stemmed succulents has been modeled in some detail for arborescent cacti from the southwestern United States. For species with a branch diameter of about 12 cm (similar to that of *E. cooperi*) and long branches of 300 cm in length (again similar to *E. cooperi*), a branch distance of about 100 cm was found to allow for 90% of maximum interception of solar radiation

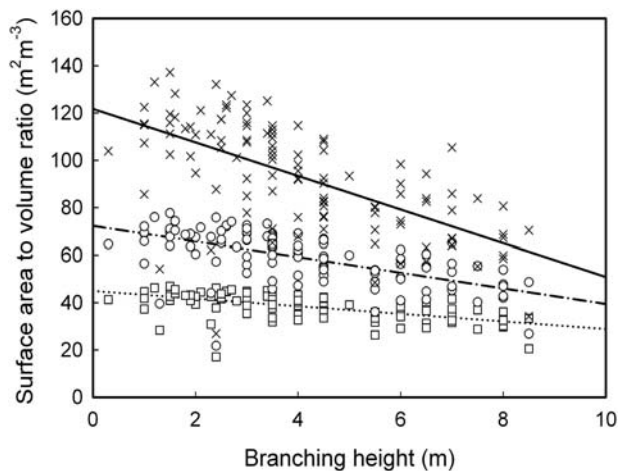


Fig. 9. Surface area to volume ratios with branching height with field data as shown in Fig. 7 (o; $y = -3.29x + 72.32$, $r^2 = 0.384$) and simulated results for a square cross-sectional morphology (squares; $y = -1.61x + 44.91$, $r^2 = 0.359$), and for a deeply fluted cross-sectional morphology (x; $y = 7.10x + 121.77$, $r^2 = 0.409$). See text for details. All graphs have a significant linear relationship with $p < 0.001$.

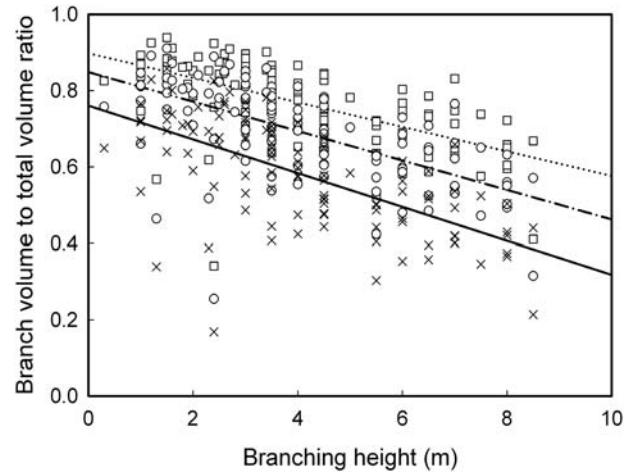


Fig. 10. Ratio of branch volume to total volume with branching height with field data as shown in Fig. 8 (o; $y = -0.039x + 0.849$, $r^2 = 0.384$) and simulated results for a square cross-sectional morphology (squares; $y = -0.320x + 0.898$, $r^2 = 0.36$) and for a deeply fluted cross-sectional morphology (x; $y = -0.044x + 0.761$, $r^2 = 0.408$). See text for details. All graphs have a significant linear relationship with $p < 0.001$.

compared with an infinite distance between branches (Geller and Nobel, 1986). Mean distances between branches in *E. cooperi* is highly variable but is typically 50–70 cm, indicating that some degree of self-shading may be present. However, extensive dieback of older branch segments is only visible in the canopies with the densest degree of branching.

The benefits of high S:V ratio in arborescent succulents are moderated by costs resulting from the need for water storage and conservation (Yeaton et al., 1980; Steenbergh and Lowe, 1983). Growth forms with a lower S:V ratio can store a larger volume of water, and may potentially utilize this water to extend the growing season (Cody, 1984; Nobel, 1994; Drezner, 2014). However, S:V ratios in arborescent cacti have been shown to exceed that required for water conservation, suggesting that increased PAR absorption may have had an important influence on the evolution of this life form (Geller and Nobel, 1984). These studies on cacti have been largely carried out in Sonoran Desert of the Southwestern United States, a warm desert ecosystem with mean annual rainfall of less than 150 mm, this environment is considerably more arid than that experienced over most of the range of tree euphorbias. Nevertheless, extended drought makes water storage a concern in adapting to stress in a long-lived perennial.

Beyond the increase in photosynthetic surface area that accrues with multiple branching, there is an added value in increasing reproductive output (Drezner, 2003). Flowers in *E. cooperi* are restricted to the ridges of the youngest branch segments. The numbers of flowers produced and their visibility to pollinators will scale directly with number of branches.

5. Conclusions

The candelabra growth form of *Euphorbia cooperi*, and likely other *Euphorbia* species with similar canopy architecture, allows these plants to add photosynthetic surface area as they grow and increase in size while at the same time minimizing problems of transpirational water loss. With age and increase in size and numbers of branches, photosynthetic surface area is added at the same time that the amount of potential storage volume to support water loss from this expanded surface area is also increasing. The key morphological trait that allows this result is the heavily suberized trunk volume that increases with size and provides added capacity for water storage without adding to surface area subject to transpirational water loss. This trait and the associated canopy architecture allows the development of increasing surface area from large numbers of branches with minimal self-shading so long as older branches are shed.



Fig. 11. Densely branched *Euphorbia cooperi* in Kruger National Park showing branch shedding which appears to be caused by self-shading. Frost damage would be expected to be most apparent on young and exposed branch tissue. Photo by Bernard Dupont.

The cross-sectional morphology of branches in *E. cooperi* clearly has selective value in balancing increased surface area with maintenance of adequate storage volume. A simulated square cross-sectional morphology would provide a “safe” solution in producing little change in S:V ratio as plants mature, but at the expense of limiting photosynthetic surface area. At the other extreme, a deeply fluted cross-sectional morphology significantly increases S:V ratio over the observed field values, especially in young plants that would potentially be more sensitive to drought stress. Cross-sectional morphology, however, has relatively little impact on the ratio of branch volume to total storage volume including the plant trunk.

Euphorbia cooperi is one of many tree euphorbias characterized by a candelabra form of growth and self-shedding of old branches. Although we have not studied other species, we hypothesize that much of the same morphological strategy of canopy architecture described here might apply to other taxa with this growth form. It would be interesting to look at intra- or interspecific gradients of variation in branch morphology and canopy architecture along a rainfall gradient. We can say much less about branch morphology and PAR absorption in other species such as *E. ingens* that have more vertically arrayed branches which they are not typically shed with age. Such a study of *E. ingens* would likely reveal interesting results.

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