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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.

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 CO_2 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; Gildenhuys, 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 (Gildenhuys, 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 thonningi*.

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 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.

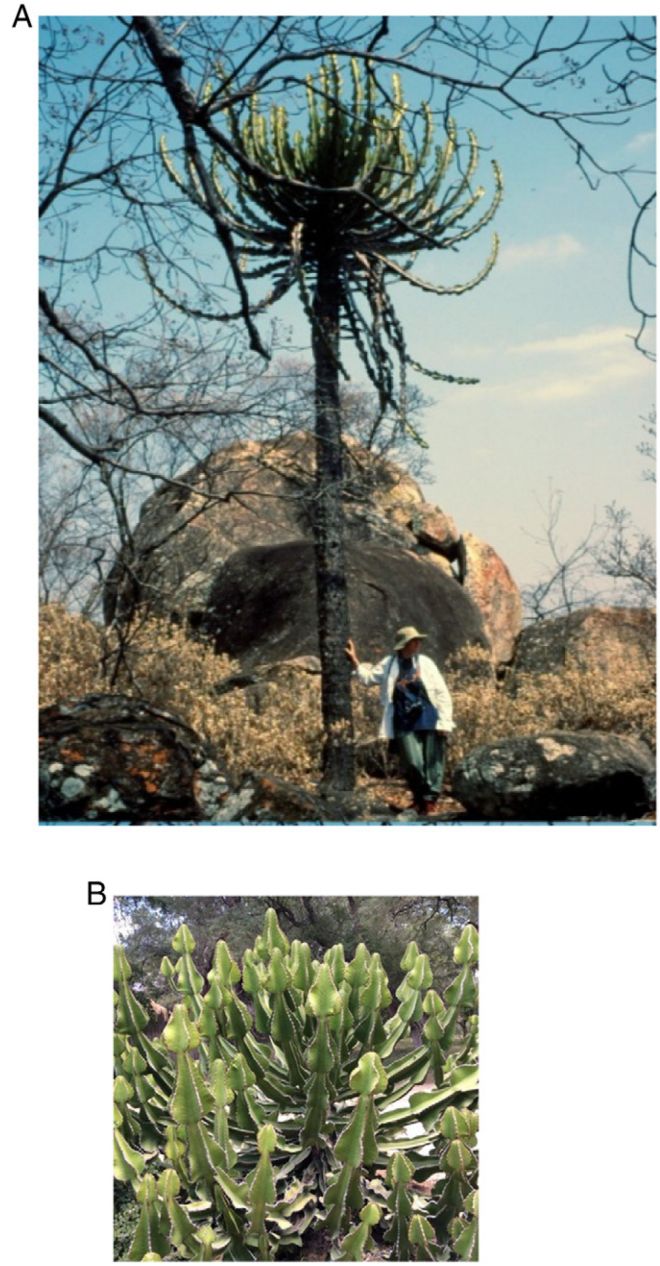

Fig. 1. *Euphorbia cooperi*: 1A. tall tree at Beaconsfield Farm, Matopo Hills; 1B. Young plant showing highly fluted branch segments. Photos P. Rundel.

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.