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Dependence of the South African geophyte *Boweia volubilis* on its inflorescence for plant carbon gain

C.E. Martin *, G. Naidoo

School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa

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A B S T R A C T

The largest organ of the eastern South African geophyte *Boweia volubilis* (climbing or sea onion) is the green inflorescence; leaves are small, ephemeral, and only occasionally produced. The reticulated inflorescence is also succulent. The goals of this study were to determine if the inflorescence of this plant is its sole source of energy and carbon, and if the inflorescence is capable of CAM photosynthesis. CO_2 exchange of all plant organs was measured and, using their total biomass, used to calculate their contribution to the carbon budget of the whole plant. Diel fluctuations in tissue acidity were also measured in the organs.

The large, green inflorescence of *B. volubilis* accounts for nearly two-thirds of the total biomass of the plant, while its occasional, linear leaves are small and ephemeral. The dominance of the inflorescence in the plant's biomass, coupled with its relatively high photosynthetic rate, illustrates the reliance of this plant on its inflorescence for nearly all its carbon gain. Although the upper part of the plant bulb is green, it cannot photosynthesize (no daytime CO_2 uptake and no O_2 release) and, thus, does not contribute to plant carbon gain. The small cotyledon and the succulent inflorescence undergo CAM-cycling, which may benefit the plant when drought-stressed.

1. Introduction

Despite the enormous variety of shapes and sizes of leaves, there is no question that the function of leaves on most non-holoparasitic plants is photosynthetic light capture and CO_2 uptake, providing the energy and carbon for all plant functions, including growth, support, and reproduction (Raven et al., 1999; Vogel, 2013). There are, of course, exceptions to this statement. For example, cactus spines are modified leaves that do not photosynthesize and instead serve to deter herbivores from attacking the succulent plant (Gibson and Nobel, 1986). Also, the small, succulent "true" leaves of cacti, as well as leaves of other plants with photosynthetic stems, e.g., species of *Ephedra*, are so small, scalelike (in *Ephedra*), and often ephemeral that their contributions to the carbon needs of the plant are negligible (Gibson and Nobel, 1986; Sofronova et al., 2014; Gorai et al., 2015).

Furthermore, although rare, some plants lack functional leaves and rely on photosynthetic roots for their supply of energy and carbon. This phenomenon has been found in species of certain orchid genera, including *Chiloschista* and *Sarcochilus* (Benzing and Ott, 1981; Cockburn et al., 1985).

In addition, reproductive structures, including flowers and fruits, are often green or have green parts on plants that rely on leaves as their primary source of energy and carbon (Werk and Ehleringer, 1983; Weiss et al., 1988; Hogan et al., 1998; Raven and Griffiths, 2015). In such cases, photosynthesis in these structures partially or fully offsets the carbon demands made on the plant for its reproduction (Werk and Ehleringer, 1983; Vemmos and Goldwin, 1993; Clément et al., 1997a, 1997b). Typically, photosynthesis by flowers and/or fruits contributes little to the carbon and energy demands of the entire plant, although inflorescences of some genotypes of *Arabidopsis thaliana* can contribute over half of the lifetime carbon gain of the plant (Earley et al., 2009). The current study reports the first known case of a relatively large plant, *Boweia volubilis*, that relies (nearly?) exclusively on its inflorescence for the entire plant's carbon supply.

Plants of the endangered *B. volubilis* (climbing or sea onion) are found in arid, shrubby vegetation and rocky desert areas in eastern South Africa (Pooley, 1998), although they are currently difficult to find in the field due to human impact (the plant is highly valued by local communities for its medicinal properties). *B. volubilis* is a perennial that comprises one or more bulbs up to 20 cm in diameter, and the uppermost part of the bulb is exposed out of the soil and is often yellowish-green. From the

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Abbreviations: CAM, Crassulacean Acid Metabolism; PPFD, photosynthetic photon flux density; vpd, vapor pressure deficit.

* Corresponding author at: Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA.

E-mail address: ecophys@ku.edu (C.E. Martin).

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middle of this exposed portion, a narrow, linear (2–3 mm wide; 5 cm long) leaf emerges annually, then is abscised after one or two weeks. The leaf is then replaced by a large, sprawling, reticulate inflorescence holding yellowish-green flowers scattered throughout the succulent, green netlike inflorescence, (Fig. 1) which can grow up to 4 m long. This flowering stem (raceme) is produced once yearly, then dies back after seed production. Thus, the inflorescence is present on the plant only about two to three months. Following its abscission, the only green tissue remaining on the plant is the small, upper, exposed portion of the bulb. Given the usual lack of leaves in the mature plant, coupled with the large size of the green inflorescence, one goal of the current study was to quantify the importance of the inflorescence in the carbon gain of whole, mature plants. In addition, because tissue succulence has often been correlated with the water-conservative Crassulacean Acid Metabolism photosynthetic pathway (Teeri et al., 1981; Ripley et al., 2013; but see Martin et al., 2009), a second goal of the study was to determine whether or not *B. volubilis* uses the CAM pathway.

Fig. 1. A flowering plant of *Boweia volubilis* in semi-natural setting in a conservation greenhouse in Durban, South Africa (A). Some of the soil around the green bulb was brushed aside, revealing some of its roots. The large reticulated green structure originating from the bulb is the inflorescence. The bulb is 5 cm in diameter. A potted flowering plant of *Boweia volubilis* in the laboratory (B). The scale is the same as in Fig. 1A. Note that the bulb is green here. An arrow points to an individual flower on the large inflorescence growing from the center top of the bulb. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2. Material and methods

2.1. Plant material

Bulbs of *B. volubilis* Harv. et Hook. (Hyacinthaceae/Liliaceae) were purchased in summer 2002 from the Silverglen Nursery, a plant conservation center operated by the Durban Parks Department, Durban, South Africa, then transported to the University of Kansas, where they were planted in soil comprising 1/3 sand, 1/3 Perlite, and 1/3 clay with a high organic matter content. Plants were not collected from the field because they are rare and protected in South Africa, as a result of overcollection by local people for medicinal and traditional use. Plants were grown in the greenhouse for at least six years under the following approximate conditions: natural photoperiod with maximum Photosynthetic Photon Flux Density (PPFD) ranging from 300 (typical) to 1000 (in sunflecks) μmol m^{-2} s^{-1}; day/night maximum air temperatures of 25–35 °C/10–20 °C, and day/night maximum vapor pressure deficits (vpd) of 3.0/1.0 kPa. Plants were watered three times weekly (once with orchid fertilizer added) and produced a vertical, linear leaf, which abscised within two weeks, followed by a large sprawling inflorescence (Fig. 1) every year. Most plants produced seeds, and these were germinated, then seedlings were grown under the same greenhouse conditions. Several months prior to experimental measurements, potted plants and seedlings were transferred to and grown in an environmentally controlled growth chamber with the same environmental conditions as in the greenhouse (lacking sunflecks), but with a 12-hour photo/thermoperiod. These plants were watered and fertilized as before.

2.2. Organ gas exchange

The plant organs were sealed into each of three gas-exchange cuvettes, which were water-jacketed for temperature control and constructed of polycarbonate to reduce CO_2 and H_2O vapor exchange between the air and the cuvette walls, for three days of nearly continuous measurements. Data for each cuvette were collected every five minutes for 20 min, then repeated after measurements of the next two cuvettes, etc. Entire leaves remained attached to the bulb, while 90% of the vertical leaf was sealed into the cuvette. The lower part of the leaf was surrounded by Fun Tak (Henkel Corp., Rocky Hill, CN) sealant putty to prevent air leakage into or out of the cuvette around the leaf base. The latter also applied to the cotyledons, although they were attached to roots instead of a bulb. Because the inflorescences were often over a meter long and nearly as wide, only a small portion could be sealed into the cuvette (0.5 l volume) using the same sealant. Previous studies in the lab found no gas exchange by the Fun Tak sealant putty. Bulbs were detached from all other plant organs, then sealed whole, with roots, inside the gas-exchange cuvettes. On the morning (0800 h) of the third day, the gas-exchange cuvettes with plant material were opened, and pieces of tissue were excised from each and frozen (-10 °C) for subsequent measurement of titratable acidity. The cuvettes were then resealed until the remaining tissue was removed at 2000 h for acidity measurement and determination of fresh and dry mass. When gas exchange of well-watered leaves and inflorescences were measured, the bulbs (roots in the case of the cotyledons) outside the cuvettes were watered daily.

Integrated daytime CO_2 uptake was calculated by measuring the area under the CO_2 uptake-vs.-time-of-day curve using the SigmaPlot 12.5 (SystatSoftware, Inc., San Jose, CA.) graphing software.

2.3. Organ O_2 exchange

Limited tissue availability restricted measurements of O_2 exchange to organs of one plant only. After tissue removal from a plant in the greenhouse (see above for conditions), tissue was sliced in buffer (50 mM MES, 1.5 mM $NaHCO_3$, pH 5.8) into sections approximately 1x3mm in size, then placed into a water-jacketted glass cuvette with