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TANK FUNCTION IN THE EPIPHYTIC BROMELIAD *CATOPSIS SESSILIFLORA*

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Abstract. Water-impounding tank bromeliads have gained a certain independence of the intermittent water supply in tree crowns, but quantitative studies on the effectiveness of these tanks to bridge rainless periods are rare. We tested the hypothesis that the vertical orientation of tanks changes during ontogeny resulting in an even stronger reduction of the effectiveness of smaller tanks than suggested by earlier studies. Observations on *Catopsis sessiliflora* (R. & P.) Mez. in a lowland forest in Panama (San Lorenzo) showed that smaller plants are indeed more horizontally oriented than larger conspecifics. Surprisingly, experimental variation of the angle of the vertical axis of a plant relative to the perpendicular of up to 60° did not affect the time until a tank ran dry. Similar to species with multi-chambered tanks, however, tank function of this single-chambered tank species was strongly size-dependent: the tanks of large plants supplied water about five times longer than those of smaller conspecifics.

Key words: *growth*, *RGR*, *San Lorenzo crane site*, *size dependency*, *water relations*.

INTRODUCTION

Lack of moisture is arguably the most important limitation for epiphytic plants, even in tropical moist and wet forests (Benzing 1990). Many epiphytic bromeliads, however, have gained a certain independence from the intermittent water supply in tree canopies by producing water-impounding foliage (= tanks). Benzing (1987) has consequently labelled these species 'continuously supplied' in contrast to the commoner, so-called 'pulse-supplied' epiphytes with a much less regular resource supply. Tanks may either consist of several separate shallow water bodies in the base of each rosulate leaf (multi-chambered tanks in genera like *Vriesea* or *Guzmania*), or feature a single central chamber formed by a tight spiral of upright leaves (in genera such as *Catopsis* or *Billbergia*).

Zotz & Thomas (1999) and Schmidt & Zotz (2001) have demonstrated that the efficiency of a bromeliad tank in bridging rainless periods is a function of plant size. For example, the smallest tanks of *Vriesea sanguinolenta* dry out eight times faster than the largest ones (Schmidt & Zotz 2001). However, Zotz & Thomas (1999) already acknowledged that *in situ* tanks may not always be oriented vertically as in their experiments, which could introduce a systematic error if orientation changes with size in tree crowns. Indeed seedlings of epiphytic bromeliads become frequently established on the underside or laterally on branches, but subsequent curvature of the stem eventually leads to an upright position of the plant (Benzing 1970). The results of a recent field study extended these earlier observations by showing experimentally that the survival of small seedlings was much greater at the side than either on the underside or upperside of branches (Zotz & Vollrath 2002). Consequently, if tanks of smaller plants are more horizontally oriented than larger ones then size-related trends in the effectiveness of tanks in bridging rainless periods may be even steeper than indicated by the above studies.

We tested this hypothesis with *Catopsis sessiliflora* (R. & P.) Mez., using a multifaceted approach. First, we localized plants at the San Lorenzo canopy crane site (Panama) and determined the angle of the water-impounding tank to the vertical. Secondly, we determined the effectiveness of *Catopsis* tanks in bridging rainless periods as a function of both plant size and angle to the vertical in a field experiment. Finally, we determined *in situ* growth and survival to be able to put our physiological results in a life-history context:

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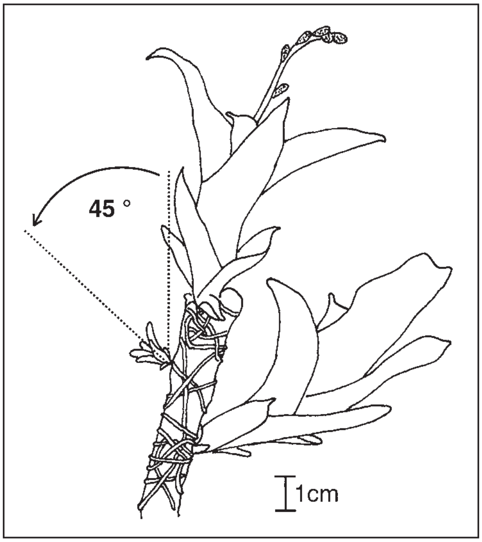

FIG. 1. Habit sketch of three *Catopsis sessiliflora* individuals growing on a twig. Also indicated is the angle of a small plant's axis relative to the vertical.

depending on how fast plants would become vertically oriented, any possibly measurable effect on the efficiency of the tank function could still be ecologically irrelevant.

MATERIALS AND METHODS

Study sites and plant material. The descriptive part of this study was conducted at the San Lorenzo canopy crane site, which is located within the San Lorenzo Protected Area near the Atlantic coast of the Republic of Panama (Wright *et al.* 2003). The average annual rainfall during the last six years was ca. 3100 mm. Canopy height of this primary lowland forest is quite variable, large trees reaching 30–40 m. The use of a small gondola allowed access to all strata of the forest. The study species, *Catopsis sessiliflora* (R. & P.) Mez., is known from moist tropical forests from southern Mexico to Brazil (Croat 1978). At the San Lorenzo canopy crane site we had located 92 individuals of this bromeliad in an area of 0.4 ha of forest during an earlier study (Zotz 2004). As documented by the following data their occurrence was restricted to the upper crowns of large trees (Zotz, unpubl. data): diameter at breast height of the 19 host trees: 49 ± 19 cm; height above ground of attachment site: 22 ± 7 m; diameter of the substratum 5 ± 3 cm (all data are means ± SD). Minimum plant size of flowering plants was 5 cm maximum leaf length (LL), and minimum size of fruiting plants was 6 cm LL. Some of these 92 plants and additional individuals were used to determine the inclination relative to the vertical and to study annual growth.

The experimental parts of the study were carried out in the laboratory clearing on Barro Colorado Island (BCI, 9°10'N, 79°51'W) in the dry season of 2004. The mean annual rainfall at this site is somewhat lower than in San Lorenzo (*ca.* 2600 mm). Detailed descriptions of vegetation, climate and ecology are given by Croat (1978).

Measurements at San Lorenzo. For a total of 61 plants ranging in size from 2 to 16 cm (longest leaf) and growing on five different trees, we determined the angle relative to the vertical, irrespective of the orientation of the substratum, with a custom-made instrument combining a plumb line and a protractor (see Fig. 1). In April 2002, a total of 72 plants was marked and measured to study *in situ* growth rates. Plant size ranged from 1 to 13 cm LL. The plants were revisited twelve months later and re-measured. A high correlation of leaf length and plant dry mass (PM (g) = 0.014 x LL (cm)$^{1.66}$; r^2 = 0.97, n = 12; Zotz unpubl.) allowed estimates of PM at the beginning and end of the 12-month period and thus the calculation of relative growth rates (RGR) in g g^{-1} day^{-1}, following Hunt (1982):

equation 1 $$RGR = (\ln PM_{t+1} - \ln PM_t) / \Delta t$$

Measurements on BCI. We collected ca. 50 individuals of *Catopsis sessiliflora* growing close to Lake Gatun on the host tree, *Annona glabra*, and transferred them to the laboratory clearing. Plant sizes ranged from 1.5 to 13 cm LL. Roots, which are known to serve primarily as holdfasts (Benzing 2000), were removed. All plants were well watered for one week to assure maximum hydration. Then a subset of 10 plants was used to determine allometric relationships of tank water capacity (TWC), plant water content (PWC), and leaf area (LA) *vs*. plant dry mass. The necessary time for a filled tank to dry out completely was determined with another 21 plants (range 1.5–12 cm LL) that were randomly assigned to one of three treatments, i.e., the vertical axis of the plant was perpendicular or deviated 30° and 60°, respectively, from the perpen-

TABLE 1. Environmental conditions during the experimental drying of filled *Catopsis* tanks.

Parameter	1st run (Mar 10–12, 2004)	2nd run (Mar 17–18, 2004)
Photon flux density (mol m^{-2} d^{-1})	27.2	40.1
Average air temperature (°C)	26.7	27.1
Average wind speed (km h^{-1})	12.2	14.0
Potential evaporation (mm)	3.6	5.5

dicular. Before the experiment, tanks were emptied three times and surfaces carefully dried with tissue paper to determine plant fresh weight with an empty tank. Starting at dawn, completely filled plants were put in small racks and exposed to the environmental conditions of the large clearing adjacent to the laboratory building and weighed at 30–60 min intervals during the day. Tanks were assumed to be empty once the predetermined weight (see above) was reached. The experiment was repeated once. The climatic conditions during the two experiments varied considerably (Table 1). For example, during the first run the average integrated photon flux density (PFD) was 27.2 mol m^{-2} d^{-1}, compared to 40.1 mol m^{-2} d^{-1} during the second run (all environmental data were provided by the Terrestrial-Environmental Sciences Program of the Smithsonian Tropical Research Institute). We also took digital photographs of all plants from above, plants themselves being vertically oriented or tilted at 60°. The projected leaf catchment area funnelling into the tank cavity was estimated by taking digital photographs and comparing the num-

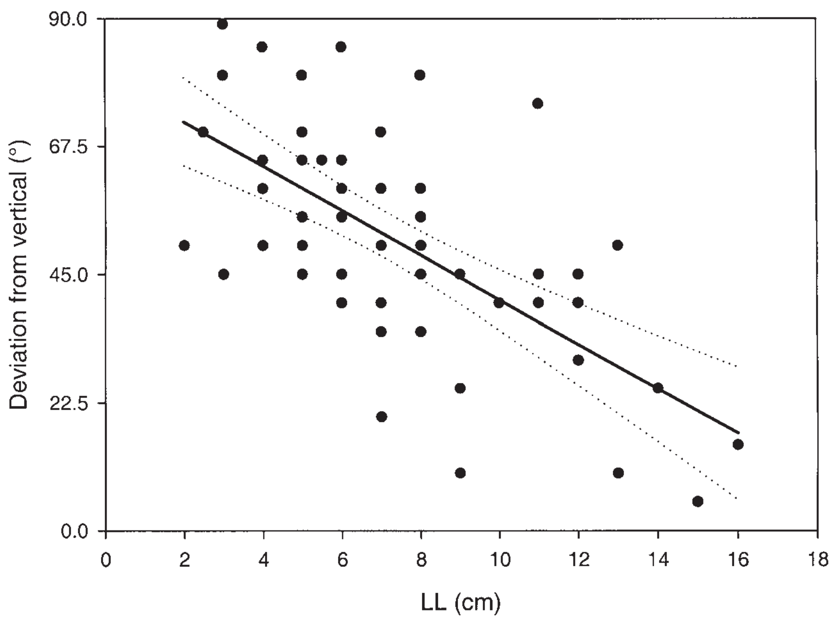

FIG. 2. Orientation of *Catopsis sessiliflora* plants in tree crown relative to the vertical. Each dot represents a single plant. Also given are regression line (solid line) and 95 % confidence intervals (dotted lines). Regression equation: deviation = 79.5 – 4 LL, $r^2 = 0.39$, $p < 0.001$, $n = 61$.

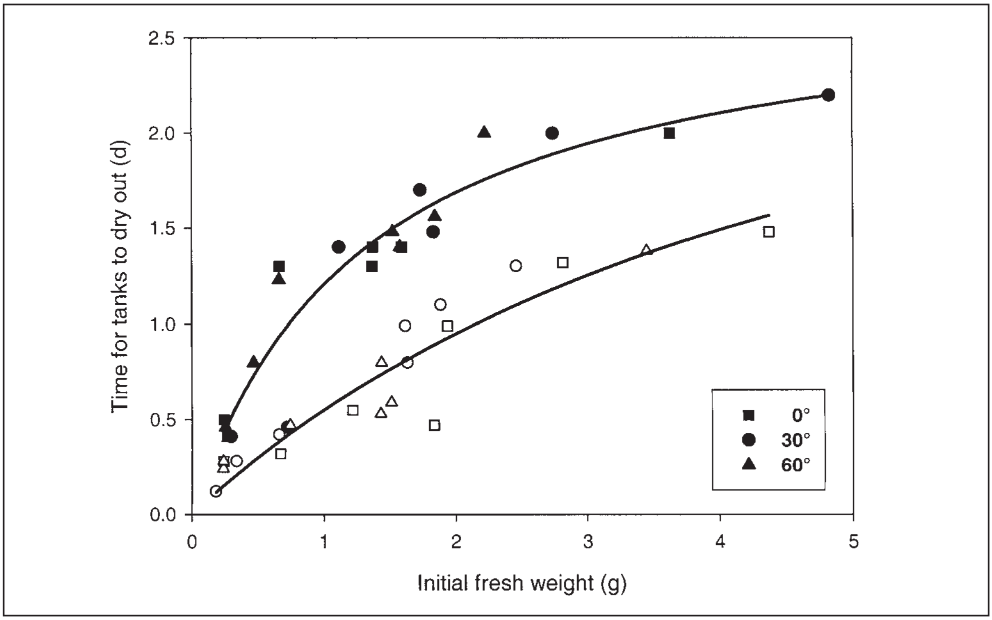

FIG. 3. The time for an initially full tank to dry out as a function of plant size and deviation from the vertical (different colors). Shown are the results of two replicate experiments (depicted by open and closed symbols). The hyperbolic functions of the form TIME = a FW / (b + c FW) explain almost 90 % of the variation (r^2 = 0.89 and 0.87).

ber of pixels of the leaf area itself and a reference area using the histogram function of Photoshop (Adobe Photoshop 6.0, Adobe, San Jose, CA, USA).

Growth under well-watered and fertilized conditions was studied for a period of two months. Plants were kept close to the laboratory building, daily integrated PFD was ca. 20 % full sunlight. Tanks were never allowed to run dry during this period, and plants were supplied with NPK fertilizer (Substral Universaldünger 18-14-18, Scotts Celaflor, Ingelheim, Germany) once a week: the NH_4^+ concentration was 38.5 mg l^{-1}; that of NO_3^- was 51.5 mg l^{-1} (compare Laube & Zotz 2003). Due to the combination of slow growth and the relatively short duration of the experiment we could not use LL as a reliable proxy of PM, but took advantage of the very close relationship of plant fresh weight and PM (r^2 = 0.97, n = 14, range = 1.5–8.5 cm LL) to calculate RGR. All statistical analyses were done with STATISTICA software (STATISTICA 5.1; StatSoft, Tulsa, USA).

TABLE 2. Size-related changes of parameters related to the water budget of bromeliad tanks. Given are equations of linear or non-linear regressions. The independent variable is plant dry mass (PM, in g).

Parameter	Equation	R^2
Leaf area (LA; in cm^2)	= 267 PM – 0.53	0.98
Plant water content (PWC; in g)	= 10.6 PM – 0.02	0.99
Tank water capacity (TWC; in g)	= 7.1 PM + 0.15	0.96
PWC / TWC (g g^{-1})	= 0.93 $PM^{-0.19}$	0.25
TWC / LA (g cm^{-2})	= 20 $PM^{-0.24}$	0.58

RESULTS AND DISCUSSION

The orientation of *Catopsis sessiliflora* plants changed with plant size (Fig. 2). The more horizontal orientation of smaller plants suggests that most successful establishments occurred laterally on branches, which was expected from earlier observational (Benzing 1970) and experimental work (Zotz & Vollrath 2002). Similar to many other members of the Tillandsioideae (Benzing 2000), seedlings of this species do not form tanks initially, but feature a spreading rosette of up to 16 rather narrow leaves. A central tank starts to form in plants with LL of about 2 cm by overlapping leaf bases. A comparison of plant water contents (PWC) and tank water capacity (TWC) reveals that these plants with small tanks rely much less on an external water supply than larger conspecifics (Table 2). While the amount of water stored in living tissues exceeded TWC two- to three-fold in the smallest plants, the ratio of PWC and TWC was about unity in mid-sized and large individuals.

Surprisingly, the orientation of a plant did not affect the time necessary for an initially full tank to run dry (Fig. 3). Plant size, on the other hand, had a pronounced effect and explained almost 90 % of the variation: the largest plants could draw upon tank water more than five times longer than the smallest individuals. The considerable variation between the two replications of our experiment was related to environmental conditions. Potential evaporation in the laboratory clearing was about 50 % higher during the second experiment (Table 1), when tanks dried out 30–60 % faster for any given size. However, our experiment clearly only partially simulated the actual conditions in tree crowns, where, e.g., strong winds will cause considerable movements of twigs and branches; epiphytes not oriented vertically may then spill substantial proportions of their tank water contents.

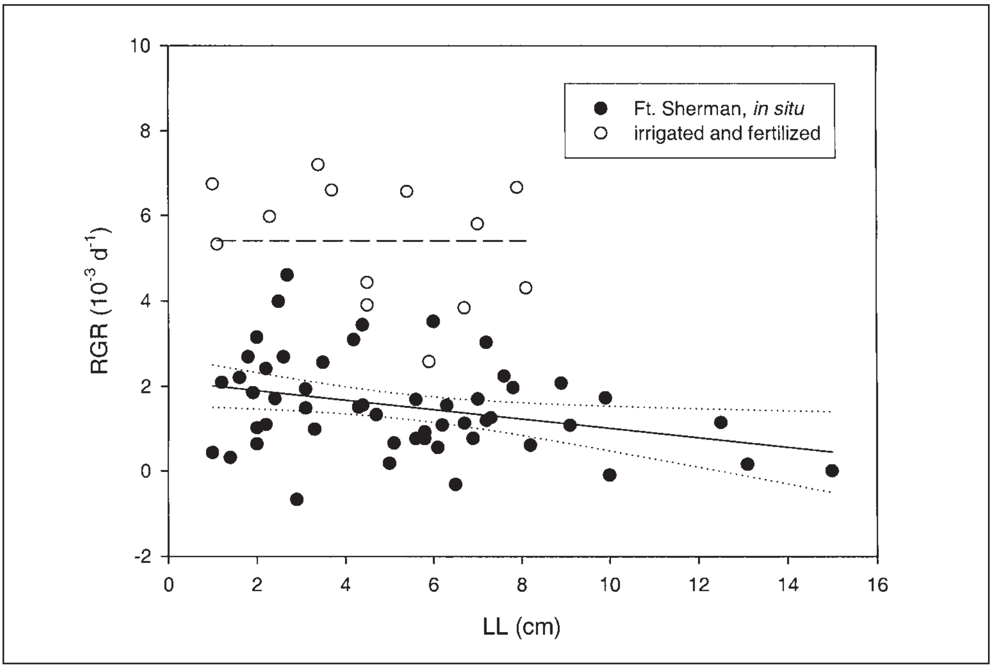

FIG. 4. Relationships of relative growth rates of *Catopsis sessiliflora* with plant size and environmental conditions. Each dot represents a different individual. Closed symbols are plants growing naturally at the San Lorenzo crane site, open symbols represent plants that were kept near the laboratory on Barro Colorado Island with a full tank and weekly fertilizing. The regression line for the San Lorenzo data (solid line) follows: RGR = 2.1 – 0.1 LL, $r^2 = 0.10$, $p < 0.05$, n = 53, dotted lines are 95% confidence intervals. The dashed line represents the average RGR of plants under near-optimal conditions.

Under the controlled conditions of the experiment, careful tilting of the plants for 30° or even 60° did not cause loss of tank water. While neither tank water capacity nor the rates of water loss were affected by the orientation of a plant, at least the filling of a tank by rainfall could be impeded. However, a comparison of the projected catchment area of individuals with a vertical orientation *vs*. 60° relative to the vertical did not yield significant differences (t-test for dependent samples; $t = -0.27$; $df = 20$; $p = 0.78$).

In situ growth rates of the 53 plants that survived from early 2002 to early 2003 (equalling an annual mortality rate of 26%) were generally low and decreased significantly with plant size (Fig. 4). Using the regressions of RGR and LL with PM, we estimated that it will take an average juvenile plant of 0.5 cm LL (i.e., the smallest individuals found in San Lorenzo) about 6 years to reach a size of 5–6 cm LL, corresponding to the minimum size of reproductive individuals. This is comparable to similar estimates for the same species growing in a montane forest in Mexico (Hietz *et al*. 2002). Consistent with other epiphytes (Castro-Hernández *et al*. 1999, Schmidt & Zotz 2002, Laube & Zotz 2003), *Catopsis sessiliflora* is inherently slow-growing: although RGR almost tripled when plants were well watered and fertilized (Fig. 4), the maximum value of RGR under these favorable growth conditions of less than 8×10^{-3} d^{-1} was still among the lowest known in the literature for any angiosperm species (Grime & Hunt 1975, Hunt & Cornelissen 1997).

To conclude, the results of this study are only partly in agreement with our initial hypothesis. While slow-growing *Catopsis sessiliflora* plants do indeed change orientation over many years, this has no functional implications under the experimental conditions. Within the range of plant sizes used in this study, the smallest tanks dried up about five times faster than the largest ones, but inclination angles between 0 and 60° had no influence on tank function.

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