

How Much Water is in the Tank? Model Calculations for Two Epiphytic Bromeliads

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Water-impounding foliage (= tank) characterizes many bromeliad species but, to date, a quantitative evaluation of the effectiveness of these structures to bridge rainless periods is not available. We present a model that analyses the capacity of these phytotelmata to supply moisture to the bromeliad as a function of plant size, and parameterize it for two epiphyte species, *Tillandsia fasciculata* and *Guzmania monostachya*. All parameters related to the recharging of a tank (e.g. catchment area, or tank capacity) and those related to water loss from the tank (e.g. tank water surface, or water absorption from the tank by the plant) changed with plant size. For both species a similar qualitative size-related pattern emerged: smaller individuals dried out much faster than larger conspecifics. Modelling the changes in tank water content for an entire year revealed that in the seasonal climate of Barro Colorado Island, Panama, tanks of smaller plants (1 g d. wt) are expected to lack water for up to 110 d (in *T. fasciculata*). Regardless of plant size, individuals of *G. monostachya* were consistently more efficient than *T. fasciculata* in maintaining moisture in their tanks. Our results provide insight into the limitations of water-impounding tanks as an adaptation to cope with an intermittent water supply typical for epiphytic habitats. These limitations are particularly pronounced for smaller individuals.

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Key words: Epiphytes, water relations, Barro Colorado Island, bromeliads, water tanks, phytotelmata.

INTRODUCTION

Vascular epiphytes, even those in wet tropical forests, inhabit a drought-prone environment. Many arboreal bromeliads have gained a certain independence from the intermittent water supply in tree canopies by producing water-impounding foliage (= tanks). These tanks, compensating for the lack of access to moisture in soil, may either consist of one central chamber formed by a tight spiral of upright leaves (in genera such as *Catopsis* or *Billbergia*, Fig. 1A) or consist of several separate shallow water bodies in the base of each rosulate leaf (e.g. in many species of *Vriesea* or *Neoregelia*, Fig. 1A). Epiphytes with either tank form have been labelled 'continuously supplied' in contrast to the more common, so-called 'pulse-supplied' epiphytes with a much less continuous resource supply (Benzing, 1987, 1990). Surprisingly, however, we cannot evaluate whether tank bromeliads do indeed have access to water and nutrients without interruption, because quantitative evidence is missing and even anecdotal information is rare. Frank and Curtis (1981) claim, for example, that at least the larger individuals of *Tillandsia utriculata* hold water at all times in southern Florida. Krügel (1993) makes a similar statement concerning the Amazonian *Guzmania weberbaueri*. Conversely, field observations in the moist tropical forest of Barro Colorado Island, Panama (BCI), indicate otherwise in many other cases (Zotz, unpubl. res.).

Plant distributions suggest a significant role for different tank forms in defining habitat preference (Gilmartin, 1973; Sudgen, 1981). Thus, a quantitative assessment of the efficacy of these phytotelmata in supplying water to the plant is highly desirable as a first step towards a comparative analysis of tank form and function. A comprehensive study of the importance of a tank as the primary source of moisture for a plant must take into account: (1) the tank capacity; (2) the catchment area for precipitation, i.e. the watershed of a plant; (3) aspects of tank geometry that influence evaporation (Benzing, 1980); and (4) how all three variables change with plant size.

We chose *Tillandsia fasciculata* Sw. and *Guzmania monostachya* (L.) Rusby ex Mez for this study, which have already attracted much interest from physiological ecologists (Martin, 1994). Both species possess a multi-chambered water-impounding tank. Based on the parameters mentioned above, transpiration data (Zotz and Andrade, 1998), and estimates of the interception of precipitation by host tree foliage (Frank and Curtis, 1981), a simulation model was developed for these two epiphytes. Using the available climate data for BCI on precipitation and potential evaporation, we were able to estimate seasonal changes in tank water content for a wide range of plant sizes, excluding only seedlings and the exceptionally large adult. The model allows us to evaluate the effectiveness of water-impounding tanks in bridging rainless periods, particularly as a function of plant size.

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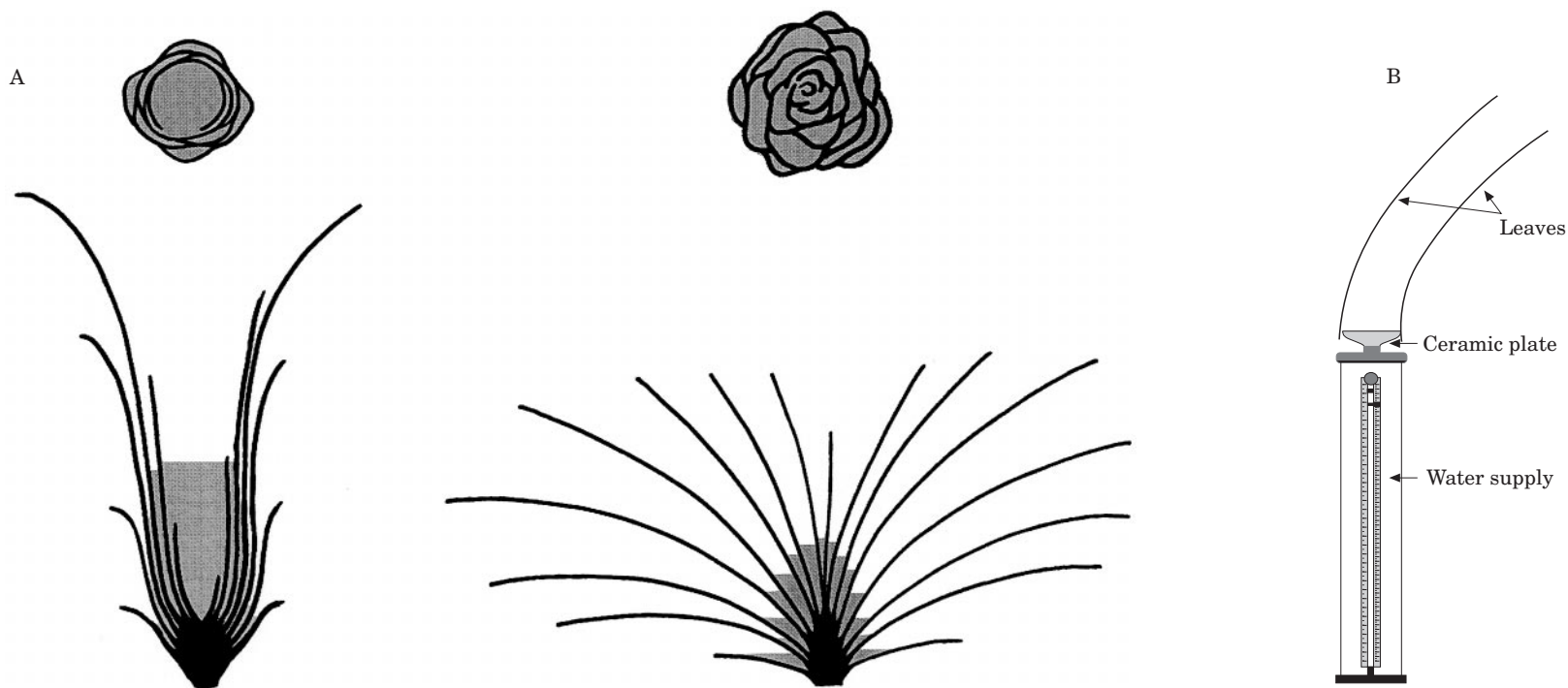


FIG. 1. A, Semi-schematic diagrams of the two main tank types in bromeliads. Bottom drawings are cross-sections of the central chamber and the multi-chamber type, respectively (shaded areas indicating water). Top drawings show the geometry of the tank water surface of the respective tank forms from above. B, Method used to estimate evaporation from a bromeliad tank. Shown is the cross section of an ETgauge with leaves of *G. monostachya* attached.

MATERIALS AND METHODS

Experiments were carried out on Barro Colorado Island (BCI, 9°10' N, 79°51' W), Republic of Panama between mid-1995 and early 1997. The vegetation of this biological reserve is classified as a tropical moist forest (Holdridge *et al.*, 1971). Mean annual rainfall is approx. 2600 mm with a pronounced dry season from late December to late April. During these 4 months completely rainless periods regularly extend for several weeks (Windsor, 1990). Detailed descriptions of vegetation, climate and ecology are reported by Croat (1978) and Leigh, Rand and Windsor (1982).

Guzmania monostachya (L.) Rusby ex Mez and *Tillandsia fasciculata* Sw. var. *fasciculata* have a wide geographic distribution: *G. monostachya* ranges from southern Florida through Peru and Bolivia, *T. fasciculata* extends from Mexico to Colombia and the Guianas (Croat, 1978). Neither species is common on BCI (pers. observ.; Croat 1978), but colonies can be quite extensive on certain hosts (e.g. *Annona glabra*, Annonaceae; Zotz, Bermejo and Dietz, 1999).

The leaf axils of both species overlap broadly and fit closely at the margins. Each body of water, which is formed by a single leaf base, has a crescent-shaped surface area. Water poured into the centre of the plant fills each axil in turn, with the excess water flowing into the axils below until capacity is reached. For the purpose of this study, tank capacity (C_{\max} , Appendix 1) is defined as the sum of the numerous small bodies of water of a shoot.

Throughout the paper, plant size is expressed in g d. wt. To help visualize plant size, we supply the regression equations of the length of the longest leaf of a plant (L , in cm) and plant dry weight (W , in g_{DW}):

$$L = 11.9 \log_{10} W + 13.1 \quad (r^2 = 0.92, P < 0.001, n = 14; G. monostachya),$$

$$L = 9.7 \log_{10} W + 17.0 \quad (r^2 = 0.93, P < 0.001, n = 15; T. fasciculata).$$

Measurements of transpiration, tank water content, and projected surface area

Correlation equations of, respectively, transpiration and maximum tank water content, and plant size were reported

for both species by Zotz and Andrade (1998, Table 1). Their data set was based on 39 plants (16 *G. monostachya*, 23 *T. fasciculata*) of different sizes (*T. fasciculata*: 0.9–65 g; *G. monostachya*: 1.0–67 g), collected from several *Annona glabra* trees. Briefly, the maximum tank water content (C_{\max}) was determined after all impounded debris had been removed from the leaf bases. After emptying the tank and drying the leaf surfaces, 24 h weight changes of entire plants exposed in the laboratory clearing on BCI were recorded to determine diel transpiratory water loss.

In addition, we took photographs of the same 39 plants from above. Subsequently, the projected leaf catchment area was estimated using Sigma Scan software (Jandel Scientific, San Rafael, CA, USA).

Water surface in the tank and evaporation rates

Evaporation from a tank is assumed to be a function of the potential evaporation on a given day and the surface area of the tank water. Evaporation from a tank was expected to be lower than from an unprotected water surface because these plants grow within a tree crown and, in addition, the tank water is somewhat protected from turbulence in the depth of the leaf rosette. We estimated the difference between potential evaporation and tank evaporation in a tree crown with the following experiment: two evapotranspiration gauges (Model A, ETgage company, Loveland, CO, USA) were hung in a 5 m tall *Annona* tree next to naturally occurring individuals of *G. monostachya* for 11 d. Then one ETgage was partially covered with leaves of a large *G. monostachya* to simulate the insulating effect of a tank, and evapotranspiration recorded for an additional 6 d. As shown in Fig. 1B, this setup probably came quite close to the natural situation (Fig. 1A).

The evaporative surface of a tank is a function of plant size and the relative tank water content. We determined the surface area by filling plants of different size with liquid gelatine (range *T. fasciculata*: 0.6–66 g; *G. monostachya*: 0.5–30 g). After hardening, the upper surfaces of each of the small bodies of gelatine were traced on paper and their area estimated gravimetrically. The water surface of a full tank is defined as the sum of all individual areas (compare Fig. 1A).

TABLE 1. Size-related changes of parameters related to the water budget of bromeliad tanks

Species	y	Equation	r^2	n	Reference
<i>T. fasciculata</i>	C_{\max} [g H ₂ O]	$C_{\max} = 1.78 W / (1 - 0.0018 W)$	0.99	23	Zotz and Andrade, 1998
	T [g H ₂ O per plant d ⁻¹]	$T = 0.30 W / (1 + 0.02 W)$	0.93	23	Zotz and Andrade, 1998
	A_{proj} [cm ²]	$A_{\text{proj}} = 8.17 + 9.74 W$	0.92	23	This study
	S_{\max} [cm ²]	$S_{\max} = 1.206 W + 1.8064$	0.99	7	This study
<i>G. monostachya</i>	C_{\max} [g H ₂ O]	$C_{\max} = 5.48 W / (1 + 0.013 W)$	0.98	16	Zotz and Andrade, 1998
	T [g H ₂ O per plant d ⁻¹]	$T = 0.90 W / (1 + 0.11 W)$	0.85	16	Zotz and Andrade, 1998
	A_{proj} [cm ²]	$A_{\text{proj}} = 34.67 W / (1 + 0.086 W)$	0.91	16	This study
	S_{\max} [cm ²]	$S_{\max} = 5.57 W / (1 + 0.072 W)$	0.99	7	This study

Equations of linear or non-linear regressions for *T. fasciculata* and *G. monostachya*, respectively, are given. The independent variable is plant dry weight (W , in g). C_{\max} (in g H₂O) is the content and S_{\max} (in cm²) is the water surface of a completely filled tank, T the 24 h transpiratory water loss [in g H₂O per plant d⁻¹], A_{proj} the projected area of a rosette (in cm²), and n is the sample size. Data used to determine the equations are from Zotz and Andrade (1998) or the present study. For both species the range of validity is 1 g–approx. 65 g in the case of C_{\max} , T , and A_{proj} , and 1 g–approx. 30 g for S_{\max} . Hence, our model is only valid for the latter range.

Model overview

The model treats the various leaf bases of the two bromeliad species as a single tank. The tank water content (C_{act}) is replenished by rain and diminished by evaporation from the water surface and uptake by adjacent foliage via epidermal scales. The following assumptions and equations are used: (1) roots play a minor role in the water relations of these bromeliads, serving primarily as holdfasts (Benzing, 1980). Plants take up water from the tank only. (2) Tanks are filled only by rain, because inputs by dew or mist are probably negligible on BCI (pers. obs.). All plants are vertically oriented. Rainfall data, obtained from the Smithsonian Tropical Research Institute for BCI (expressed as g cm^{-2} ground surface), are corrected for interception losses by host tree foliage. The percentage of throughfall (F) is calculated after Frank and Curtis (1981):

$$F = 0.88 \text{ rain}(\text{g cm}^{-2})$$

Precipitation events of ≤ 1 mm are assumed to be completely intercepted by tree foliage. This calculation applies for certain small tree species and we assume its validity for *Annona glabra* as well. The formula could easily be adapted to any other situation. (3) Water input is a function of both the amount of throughfall (F) and the projected area of a plant (A_{proj} , in cm^2). The latter depends on plant size. The model assumes that all precipitation hitting a leaf is channelled into the leaf bases, i.e. fills the tank. Tanks can be filled to a maximum (C_{max} , in $\text{g H}_2\text{O}$ per plant), which is provided by Zotz and Andrade (1998, see also Table 1). (4) Tanks lose water either by evaporation or water uptake by the plant via absorbing scales (Benzing, 1980). The evaporative losses from a tank (E_{tank} , in g water per plant) are estimated as:

$$E_{\text{tank}} = k S_{\text{act}}(\text{m}^2) E_{\text{pot}}(\text{g m}^{-2}), \quad (1)$$

where k is the ratio of the evaporation rates in a tank *vs.* those of an unprotected open surface, S_{act} the water surface in a tank, and E_{pot} the potential evaporation. The water surface in plants is estimated from equation:

$$S_{\text{act}} = (C_{\text{act}}/C_{\text{max}}) S_{\text{max}}, \quad (2)$$

where C_{act} is the actual water content, C_{max} the maximum water content and S_{max} the maximum surface of water when the tank is full. No further corrections for changes in E_{tank} with decreasing tank water level were included in the model. In our model, the amount of water a plant loses by transpiration (T) is taken up from the tank. We assumed that a plant with a water-filled tank would show the same transpiration rates as during the first 24 h after emptying the tank. This allowed us to use the data of Zotz and Andrade (1998) on plant water loss during the first day of a drought cycle for our model. No data are available on the relationship of transpiration rates of well-watered plants on days with different evaporative demand. In our model, we used the maximum 24 h transpirational water losses only on rainless days with free evaporation > 3 mm, i.e. $E_{\text{pot}} > 3 \text{ kg m}^{-2}$. On partially cloudy days ($1 \text{ mm} < E_{\text{pot}} < 3 \text{ mm}$) or days with rain < 5 mm, transpiration was set to 66 % of this maximum value; on rainy days with precipitation exceeding 5 mm,

transpiration was set to zero. (5) Thus, the tank water content on a given day (C_{dayn} , in $\text{g H}_2\text{O}$) depends on that of the preceding day ($C_{\text{dayn-1}}$) in the following way:

$$C_{\text{dayn}} = C_{\text{dayn-1}} + (F A_{\text{proj}}) - E_{\text{tank}} - T \quad (3)$$

where plant projected area (A_{proj}), the maximum 24 h transpiration rates (T), and the evaporation from the tank depend on plant size (E_{tank}), while throughfall (F) is primarily a function of the canopy architecture (see above). (6) For consistency, the model is valid for a size range of 1–30 g_{DW} in both species.

RESULTS

Parameter estimates

Although a number of regression equations for the parameters needed in our model were already available (Zotz and Andrade, 1998), others, e.g. the relationship of the projected area of an individual specimen with plant size, had to be determined (Fig. 2). An overview of all the regression equations that enter the model is provided in Table 1. In all cases we detected highly significant size-related changes in the parameter of concern, most relationships being non-linear. An especially important parameter in our model is the estimate of the evaporation rate of the water in a tank [compare eqn (3)]. In order to be able to use the available data of potential evaporation on BCI, we compared the evaporation rates of a partially protected ETgage and an unprotected ETgage. On average, an ETgage in the crown of an *Annona glabra* tree lost only about 70 % of the water of the unprotected one ($72.3 \pm 14.5\%$, mean \pm s.d., $n = 11$ d). Protection by leaves of *G. monostachya* further reduced the evaporative losses by about a quarter to $55.0 \pm 11.3\%$, (mean \pm s.d., $n = 6$ d) of the unprotected control in the open. Hence, our model uses the evaporation data of a free water surface corrected for these percentages [equation (1): bromeliad alone, $k = 0.76$; bromeliad within the crown of *A. glabra*, $k = 0.55$].

Model validation

We tested our model by directly determining the necessary time for a filled tank to dry out completely. The experiment was repeated once in the dry season and again in the rainy season for a total of 15 and 18 plants of *G. monostachya* and *T. fasciculata*, respectively. As shown in Fig. 3, the measured time periods closely matched the expectations in *G. monostachya*. In *T. fasciculata*, however, the time needed for a tank to dry out was consistently shorter than expected from the model.

Model predictions

The possible amount of water charging a tank depends on the amount of water already present there, the amount of rainfall (corrected for interception losses), and tank capacity. Figure 4 shows that the rainfall necessary to fill a tank increases with plant size, much more so in *G. monostachya* than in *T. fasciculata*. Precipitation of about 5 mm or, respectively, 6 mm (when taking interception losses into

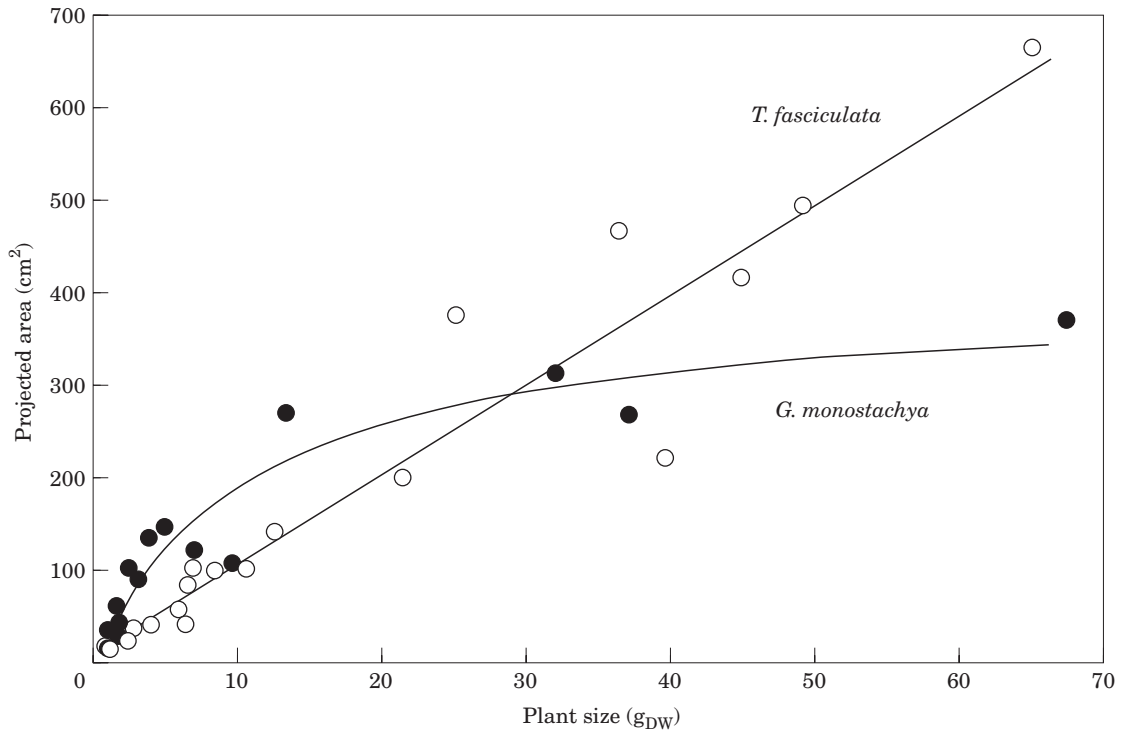


FIG. 2. Changes in the projected area of two tank bromeliads with size. Shown are the results of 16 (*G. monostachya*: 1.0–67 g_{DW}, ●) and 23 determinations (*T. fasciculata*: 0.9–65 g_{DW}, ○), respectively, and the best-fit regressions (compare Table 1).

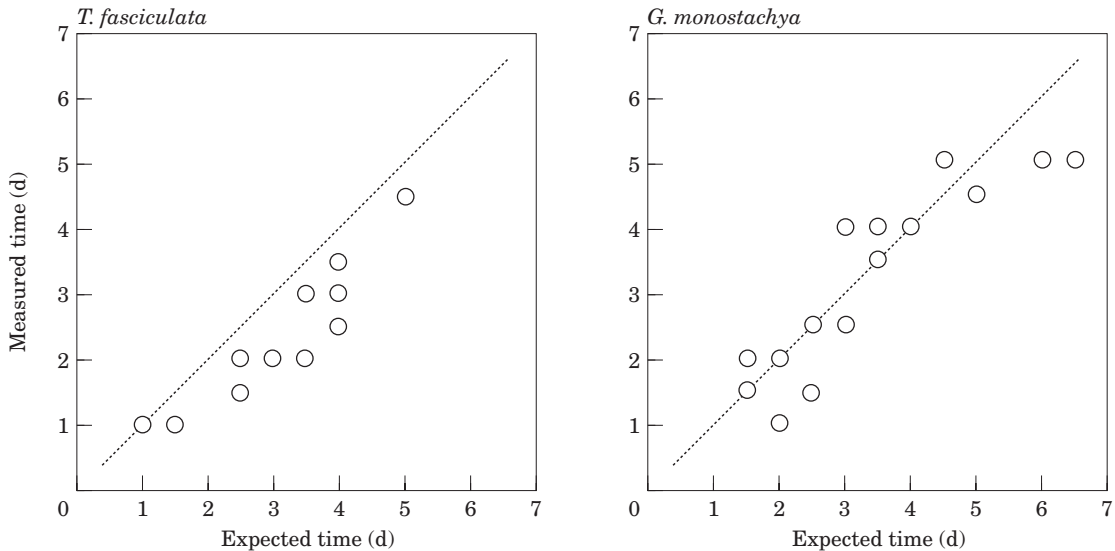


FIG. 3. Comparisons of the expected (calculated using the model) and the observed time (in d) for a full tank to dry out. The dotted line represents a one-to-one match.

account) will fill an empty tank of even the largest *G. monostachya*. Much less rain is necessary to fill the tank of a large *T. fasciculata*, i.e. less than 2 mm.

Water is subsequently lost from the tank by both evaporation and plant absorption, the latter assumed to equal whole plant transpiration. The relative importance of those two processes for changes in tank water content is analysed in Fig. 5. Assuming a full tank with a maximum water surface (S_{\max}) and a potential evaporation rate of

4 mm (the average daily evaporative rate for BCI; Windsor, 1990), losses via evaporation always exceeded losses to the plant. The ratio of evaporation to transpiration (i.e. absorption by the plant) increases with plant size: it ranges from approx. 1.5–1.9 in *T. fasciculata* and 1.8–2.4 in *G. monostachya*.

The relationships of the different water relations parameters with plant size presented until now allow us to simulate the long-term changes in tank water status. We

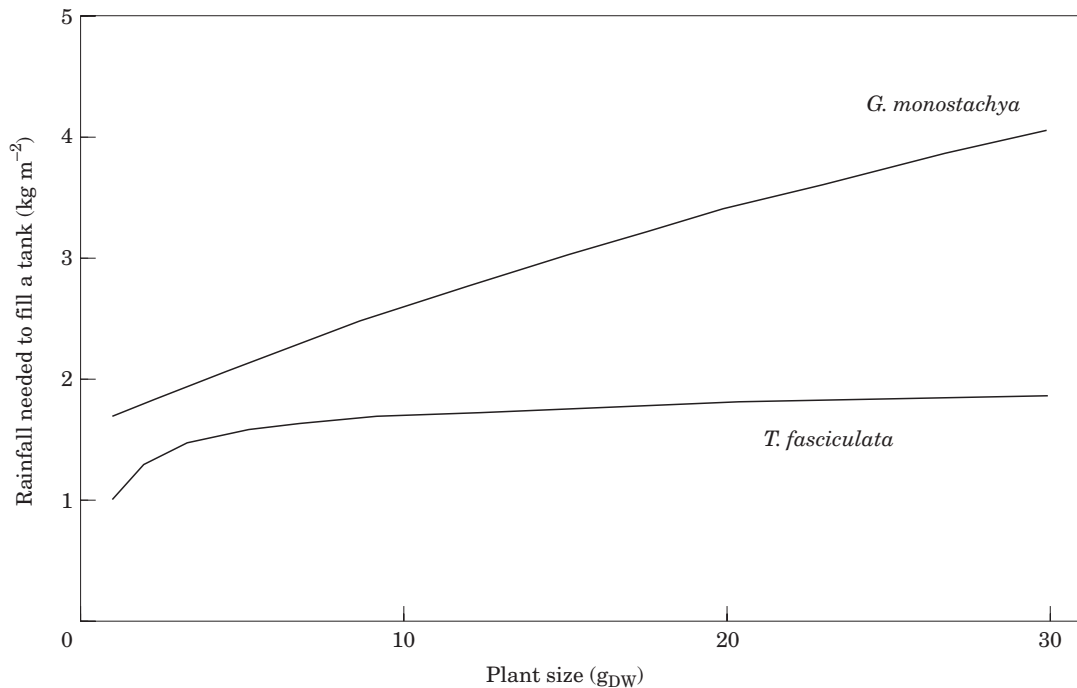


FIG. 4. Model predictions: amount of rainfall (in $\text{kg m}^{-2} = \text{mm}$) needed to fill an empty tank of *G. monostachya* and *T. fasciculata* as a function of size.

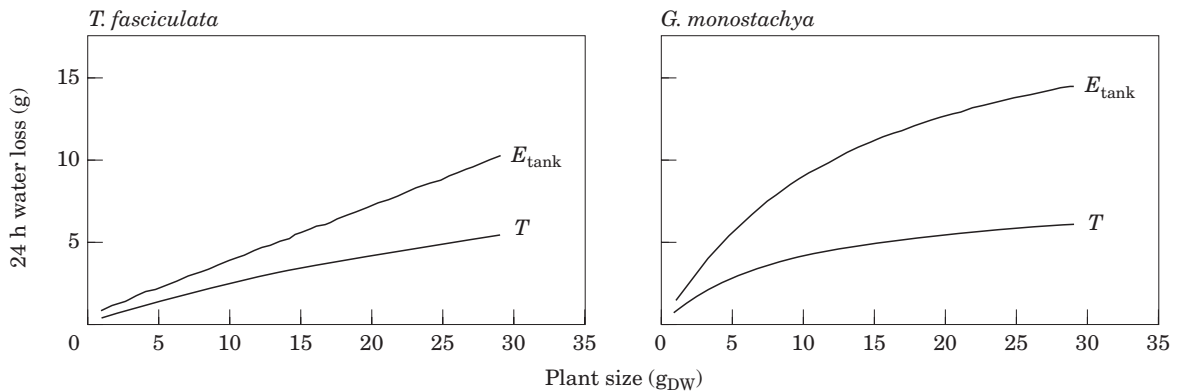


FIG. 5. Model predictions: size-related changes in water loss from a full tank due to evaporation (E_{tank}) and due to absorption of water by the plant (assumed to equal plant transpiration, T). The evaporation rate was assumed to be 70% of the long-term average from an open water surface ($= 4 \text{ kg m}^{-2}$).

chose 1995, a year with an annual amount of precipitation (2530 mm) comparable to the long-term average of approx. 2600 mm. Our plants were assumed to be growing within the crown of *A. glabra*, hence evaporation from the tank was taken as 55% of that of an open surface. Figure 6 shows the results of our simulation for both *G. monostachya* and *T. fasciculata* for a small (1 g_{DW}) and a large plant (30 g_{DW}). In plants of all sizes and both species, the tanks of these bromeliads completely dried out for at least a few days during the course of this year. The relationship between plant size and the number of days with an empty tank in 1995 is shown in Fig. 7. Although the relative size-related changes were comparable in both species, the absolute number of days with empty tanks was consistently larger in *T. fasciculata*. For example, the smallest individuals included

in the model (1 g_{DW}) were expected to have been without water on almost every third day of the year, i.e. about 20% more often than in a *G. monostachya* of similar size. The differences between the two species are even more pronounced among larger individuals (30 g_{DW}). While our model estimates about 1 month with an empty tank for *G. monostachya*, tanks of *T. fasciculata* were dry for more than 2 months in total. Possibly more important than the total number of days with an empty tank during the year is the maximum number of consecutive days without a tank reserve. The longest time period with an empty tank was identical in small individuals (1 g_{DW}) of both species, i.e. 17 d, but different in larger plants (30 g_{DW}), i.e. 16 d in the case of *T. fasciculata* and 12 d in *G. monostachya*.

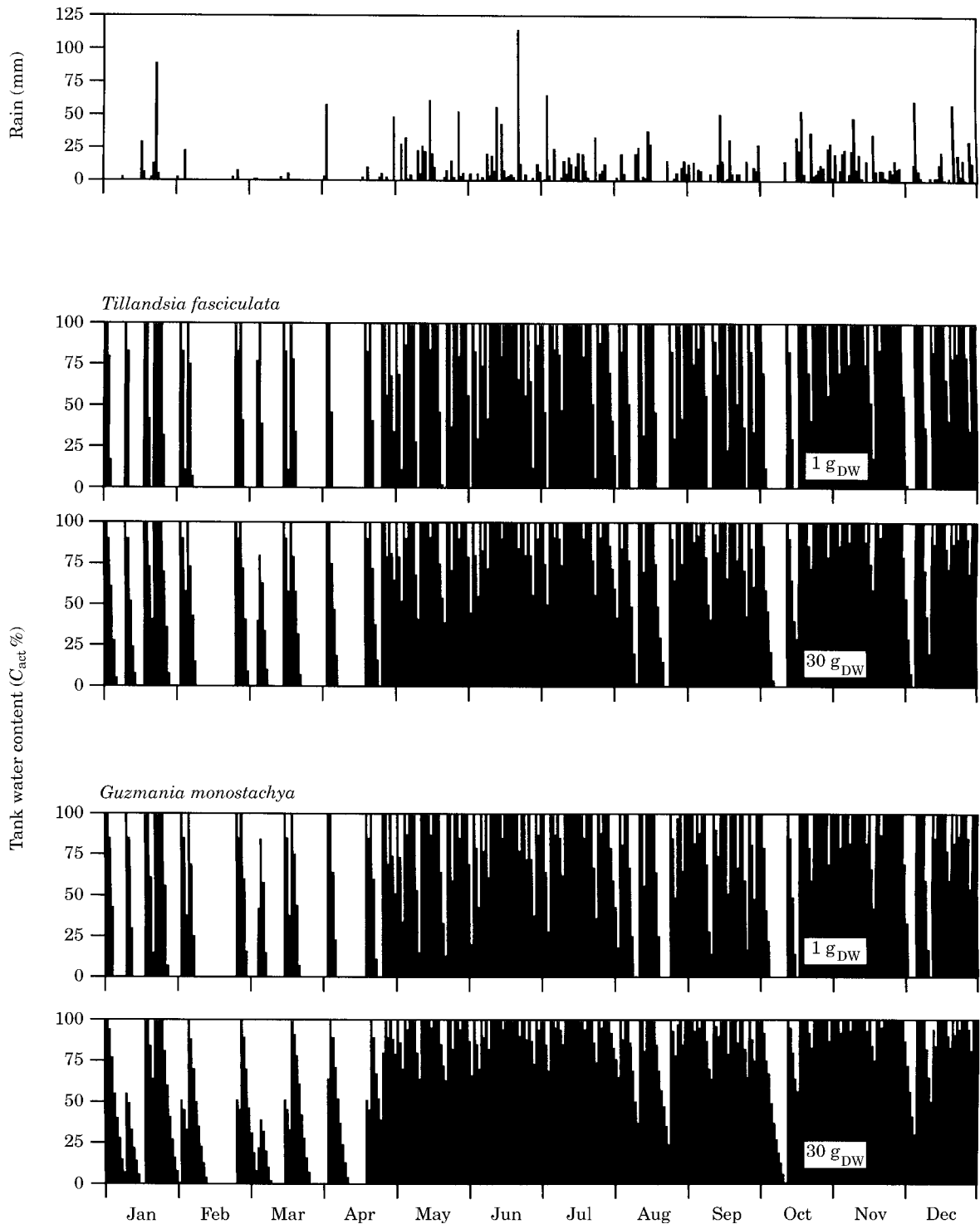


FIG. 6. Model predictions: simulated annual changes in the tank water status (in % of a full tank, C_{\max} %) of two bromeliads for 1995. Shown are the rainfall patterns for Barro Colorado Island, and the relative changes in C_{act} for a small ($1.0 \text{ g}_{\text{DW}}$) and a large (30 g_{DW}) individual of *T. fasciculata* and *G. monostachya*, respectively.

DISCUSSION

Tank bromeliads have received considerable attention from ecologists, but primarily because of the diverse animal communities they host in their phytotelmata (e.g. Picado,

1913; Laessle, 1961; Fish, 1976; Frank, 1983) and much less so because of their unusual ecophysiology (Adams and Martin, 1986; Benzing, 1990). More than a decade after Benzing distinguished 'continuously-supplied' and 'pulse-supplied' epiphytes, we still have no data on what

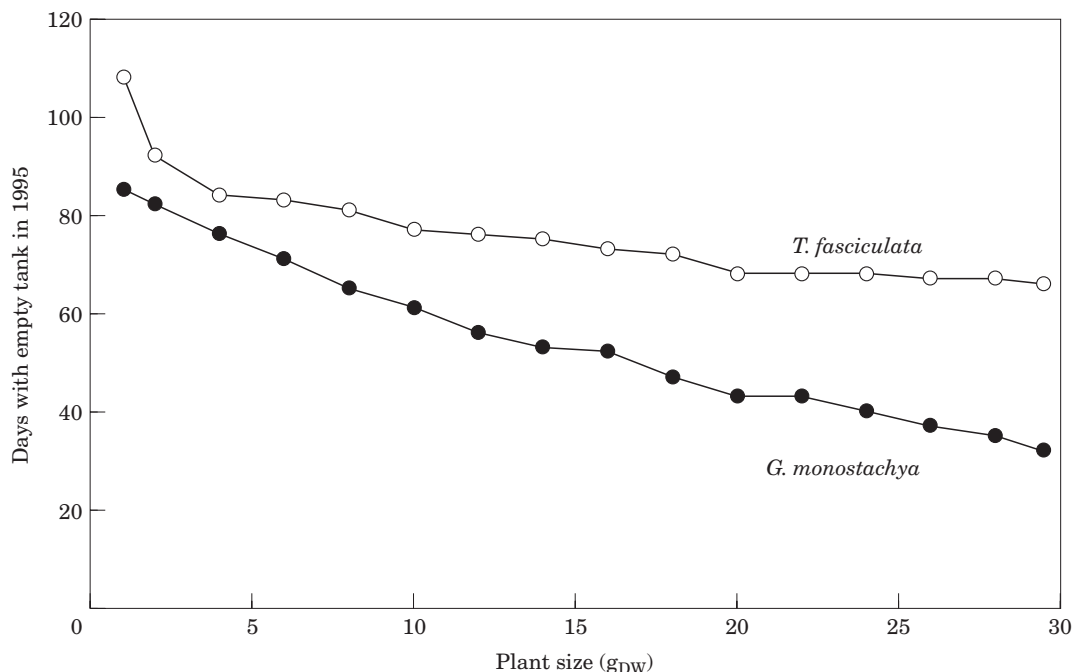


FIG. 7. Model predictions: the number of days with an empty tank in 1995 as a function of size. Shown are the results of 32 simulations of annual changes in the tank water status of *T. fasciculata* (○) and *G. monostachya* (●) (compare Fig. 6).

‘continuous’ means in the real world. The only sources of information are anecdotal in nature (e.g. Frank and Curtis, 1981; Krügel, 1993). However, the development of the model presented here was not only motivated by an interest in the ‘efficacy’ of water tanks to bridge rainless periods, but also by a conceived lack of attention to the importance of plant size in the study of the ecophysiology of vascular epiphytes in general. We have already demonstrated that important physiological parameters related to photosynthesis (Zotz, 1997; Zotz and Ziegler, 1999; Zotz, Stuntz, Schmidt, unpubl. res.) or plant water relations (Zotz and Tyree, 1996; Zotz and Andrade, 1998) change with plant size. If we are to understand the mechanisms allowing plants to grow and survive in sometimes very exposed parts of tree crowns we have to include, if not actually focus on, the most vulnerable stages of the life cycle, i.e. the smaller and younger plants.

Although the current version of our model has limitations, we believe that future refinements will not alter our general conclusions. All parameters utilized in the model show size dependent changes (Table 1, Fig. 2). Thus, it is not surprising that all derived aspects of plant water relations, including the number of days a plant can sustain maximum transpiration rates with one tank filling (Fig. 3), the ratio of evaporation from the tank to plant transpiration (Fig. 5), the frequency of days with an empty tank *in situ* (Fig. 7), or the amount of rain necessary to fill a tank (Fig. 4), vary with plant size.

Our results clearly indicate that these two bromeliads are not ‘continuously supplied’. Denied irrigation, even the tanks of large individuals of *T. fasciculata* and *G. monostachya* will dry out after a few days or after little more than 1 week, respectively. In an ‘average’ year like 1995, rainless

periods of 2 or more weeks are quite normal (Windsor, 1990). Hence, plants of all sizes must tolerate extended periods without external water supply. We have already studied the transpiration of both species with an empty tank (Zotz and Andrade, 1998): rates fall rapidly, reaching a minimum after 4–5 d. Subsequently, they lose about 2% of their plant water content per day. Zotz and Andrade’s (1998) results and those of the current study prompt us to inquire how much time is required for a fully charged plant to lose all its tank water and approx. 50% of the water stored in tissues. Assuming a daily evaporation rate of 4 mm (which is the long term average for BCI; Windsor, 1990), plants growing in the crown of *A. glabra* [i.e. k of 0.55, eqn (1)] would reach this stage after about 30 d in the case of a large *G. monostachya* (Fig. 8), but in not less than 40–50 d, or about 50% later, in a large *T. fasciculata*. In the dry season, rainless periods lasting more than 4 weeks may occur in certain years (Windsor, 1990). Nevertheless, even drought of this length would probably cause no problem for larger plants of either species, because both *T. fasciculata* and *G. monostachya* tolerate a tissue water deficit of 50% or more (Zotz and Andrade, 1998). Smaller plants, however, in particular small *G. monostachya*, will have reached very high, possibly lethal, levels of desiccation after the same rainless period.

The tanks of *T. fasciculata* are not as effective in bridging the time between rainfall events as those of *G. monostachya*. During 1995, the smallest individuals included in our study (1 g_{DW}) must have experienced 108 d with an empty tank in the former, but only 85 d without external water supply in the latter case (Fig. 7). The number of days with an empty tank should be compared to the number of days without rain: in 1995, rainfall exceeding 2 mm occurred on 155 d.

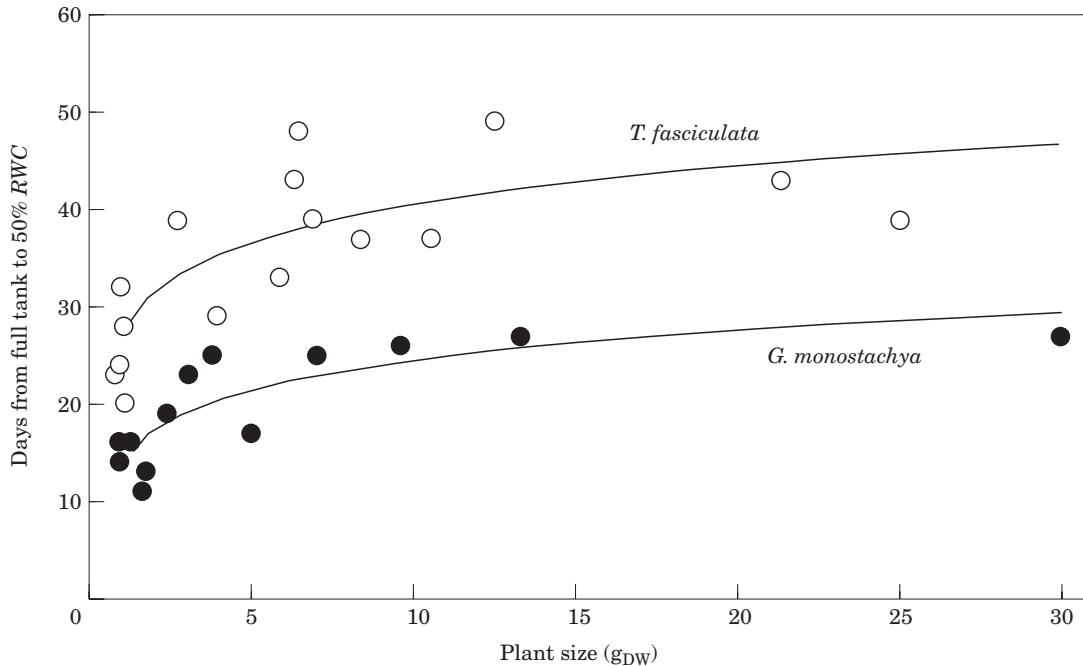


FIG. 8. Model predictions: the number of days for a plant with a fully charged tank to dry out and lose 50 % of its tissue water content (RWC, compare Zotz and Andrade, 1998). Assumptions: $E_{\text{tank}} = 70\%$ of the average BCI evaporation rate ($= 4 \text{ kg m}^{-2}$). Maximum transpiration (T) when $C_{\text{act}} > 0$, then reduced T as described in Zotz and Andrade (1998). \circ , *T. fasciculata*; \bullet , *G. monostachya*. For more details see text.

Consequently, tank water was available for small plants on only 50 % of the approx. 200 dry days. Larger individuals must have experienced less deprivation.

Smaller plants have higher ratios of evaporative surfaces to internally and externally stored water (Zotz and Andrade, 1998). Thus, although smaller plants are at a disadvantage in almost all aspects of their water relations compared to larger conspecifics, less rainfall is needed to recharge them (Fig. 4). This advantage is of little ecological bearing, however, because small rain events are probably almost completely intercepted by the tree canopy and most rainstorms on BCI are heavy enough to fill even the largest tanks of the two species anyway, i.e. exceed 6 mm (Fig. 4, compare Windsor, 1990).

Limitations of the model

The present model was designed to simulate two particular species of bromeliads. We do not claim that our results allow generalizations concerning the value of a tank for other epiphytic species to bridge rainless periods in similar vegetation, let alone other forest types. In fact, several points must be further refined in the analysis of the two species in focus. For example, the model treats transpiration rates as independent of tank water status as long as some water remains. It is conceivable, however, that transpiration rates decline as soon as the tank level has reached a critical level, although data for *Vriesea sanguinolenta* (Schmidt and Zotz, unpubl. res.) indicate that our assumption is indeed valid. Moreover, the treatment of the separate volumes of water in multiple leaf bases as a single entity is not realistic. Some bodies of water, especially those in the centre of a plant, may hold water much longer than others (Thomas,

pers. observ.). We are not sure about the biological significance of this observation, but suggest advantages for the younger, more vulnerable parts of the plant.

The maximum water content of a tank may actually be smaller in a natural setting than assumed by the model due to accumulated organic material (in the model, organic material in the leaf bases is ignored) or due to the non-vertical orientation of the plants. However, these deviations from *in situ* conditions will not influence our conclusions unless, for example, the relative amount of detritus in smaller and larger plants differed considerably. If, for example, larger plants collected proportionally much more organic material than smaller plants, then the differences between smaller and larger plants, e.g. in the number of days with an empty tank, could be smaller than suggested by the model.

Finally, our estimate of the evaporation rate from the tank was based on measures with leaves of *G. monostachya*. Using the same ratio of $E_{\text{tank}}/E_{\text{pot}} [= k, \text{eqn (1)}]$ for *T. fasciculata* could be the reason for the discrepancy between the expected and the observed time for a tank to dry out (Fig. 3). The latter species has more shallow and more open bodies of water and thus probably a different k . Changing k , e.g. from 0.7 to 0.9, reconciles expectations and observations for this species (data not shown). However, future research should not only aim at a refinement of the current model. Tank shapes obviously reflect a compromise between light interception, water impoundage and nutrient relationships. A more useful model—applicable to a wide range of different tank forms—should incorporate all of these possibly conflicting aspects of tank architecture, analyse trade-offs between functions, and thus allow us to address the interesting question of the biological significance

of the diverse shapes and sizes of tanks characteristic of the Bromeliaceae (Benzing, 1980).

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APPENDIX 1

List of symbols

A_{proj}	Projected area of a plant
C_{act}	Actual tank water content
C_{max}	Tank water capacity
E_{pot}	Potential evaporation
E_{tank}	Evaporation from the tank
F	Throughfall
k	Ratio of evaporation rates from a tank <i>vs.</i> potential evaporation
L	Length of the longest leaf of a plant
S_{act}	Water surface of a tank (= evaporative area)
S_{max}	Maximum water surface of a (full) tank (= maximum evaporative area)
T	Whole plant transpiration rate
W	Plant dry weight