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UNUSUAL WATER RELATIONS IN THE CAM ATMOSPHERIC EPIPHYTE TILLANDSIA USNEOIDES L. (BROMELIACEAE)

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Past studies have reported two unusual aspects of the water relations of the atmospheric CAM epiphyte *Tillandsia usneoides* L. (Bromeliaceae): a drought stimulation of nocturnal CO_2 uptake, and nocturnal absorption of water vapor. Contrary to past reports, a 10-d drought did not stimulate nocturnal CO_2 uptake in this species. On the other hand, previous reports of nocturnal water vapor absorption were confirmed in situ throughout a year, although tissue hydration from this source was insufficient to offset daytime water loss. Deposition of dew on the plants was never observed in the field. It is hypothesized that the unusual nature of the water relations of *T. usneoides* is attributable to the interactions between two "pools" of water and the external atmosphere. The dense indumentum of trichomes obscuring the surface of this epiphyte comprises one pool and is most likely responsible for rapid hydration early in the night and dehydration early in the day. In addition, stomata control water loss from the living mesophyll cells, the second pool, for the remainder of the night. The high rates of water loss observed throughout the day when stomata are closed probably result from leakage through the trichomes.

Introduction

Based on their life forms, most epiphytic members of the Bromeliaceae can be divided into two main groups—the tank and atmospheric types (BENZING 1973, 1980). The former species possess broad, rosulate leaves whose bases overlap such that numerous, small catchments intercept and retain water as well as plant and animal detritus. Tank-forming epiphytes and their terrestrial counterparts exhibit similar water relations (BENZING and RENFROW 1971; ADAMS and MARTIN 1986). On the other hand, the atmospheric-type bromeliads, with reduced, highly absorptive shoots, have no external source of water, except during rains, and some, such as *Tillandsia usneoides,* lack specialized water storage tissue (BENZING and RENFROW 1971). Thus, atmospheric epiphytes are likely to experience drought frequently, especially if rainfall frequency is erratic. Vulnerability to desiccation is to some degree reduced by Crassulacean acid metabolism (CAM) (BENZING 1980), a characteristic of all atmospheric epiphytes and many other inhabitants of arid habitats (KLUGE and TING 1978). In addition to physiological adaptations which minimize drought stress, the very thick boundary layer resulting from the dense indumentum of trichomes on atmospheric epiphytes presumably further restricts water loss by increasing leaf boundary layer thickness (BENZING et al. 1978; LÜTTGE et al. 1986; but see JOHNSON 1975).

The few investigations of the water relations of atmospheric epiphytes have reported two unusual findings. Unlike all other higher plants, these epiphytes reportedly absorb substantial amounts of water vapor from the atmosphere (SCHIMPER 1884, 1888; PICADO 1913; PENFOUND and DEILER 1947; VIRZO DE SANTO et al. 1976). Little work has been reported beyond these earlier findings. Furthermore, such unusual behavior has not been reported in three atmospheric species of *Tillandsia* in two studies (BIEBL 1964; BENZING and DAHLE 1971). To further complicate matters, water vapor exchange data have been conspicuously absent from studies of gas exchange in these plants. Instead, brief statements are made about difficulties in measuring the low rates of water vapor exchange as well as indications of, but no data on, brief periods of water vapor uptake and loss (LANGE and MEDINA 1979; MARTIN and SIEDOW 1981; MARTIN and PETERS 1984; MARTIN and ADAMS 1987). The putative absorption of water vapor at night is difficult to reconcile with the physiology (CAM) of atmospheric epiphytes. Given normal water potential gradients, it seems highly unlikely that water vapor is absorbed by the plant when the stomata are open at night.

There are several reports of an unusual drought-induced enhancement of nocturnal CO_2 uptake in *Tillandsia usneoides*. Diurnal measurements of CO_2 exchange in this species clearly showed increased rates of nocturnal CO_2 uptake in plants at 80.2% tissue water content compared with those at 82.3% (KLUGE et al. 1973). Based on these findings, several authors have concluded that modest tissue desiccation sometimes enhances CAM activity (MEDINA et al. 1977; KLUGE and TING 1978). Further studies with *T. usneoides* have supported this conclusion. In situ measurements of nocturnal CO_2 uptake in plants in North Carolina indicated that lower tissue water contents during rainless periods were not correlated with decreased CAM activity (MAR-

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TIN et al. 1981), as is usually the case (SZAREK and TING 1975; HANSCOM and TING 1978; KLUGE and TING 1978). Finally, plants monitored in the laboratory exhibited higher rates of nocturnal CO_2 uptake following wetting, relative to rates with the same plants before wetting (MARTIN and SIEDOW 1981).

This reported drought enhancement of CAM does not occur in two other atmospheric CAM epiphytes. Rates of nocturnal CO_2 uptake in the atmospheric bromeliad *T. schiedeana* were not stimulated by decreasing tissue water content following wetting (MARTIN and ADAMS 1987). Also, photosynthetic O_2 evolution in excised, sliced leaves of *T. ionantha* was not stimulated by decreasing tissue hydration (BENZING and DAHLE 1971).

Given the unusual and conflicting findings of past studies, the research reported here was designed to investigate further the water relations of the atmospheric epiphyte *T. usneoides*. The following questions were addressed: (1) does decreasing tissue water content enhance nocturnal CO_2 uptake? (2) is water vapor absorption a common phenomenon in situ? and (3) when is water absorbed and can the absorption offset losses? The results indicate that CAM in *T. usneoides* is not enhanced by desiccation, nocturnal water vapor absorption is common in situ, and absorption rarely equals losses.

Material and methods

DESICCATION EFFECTS ON CO_2 EXCHANGE

Clumps of *Tillandsia usneoides* were collected from trees approximately 50 km west of Corpus Christi, Texas, in January 1983 and then grown at least 6 mo in the University of Kansas greenhouse. Greenhouse conditions varied throughout the year but were approximately 1,000 μmol $m^{-2}s^{-1}$ maximum photosynthetic photon flux density (PPFD), measured with a LI-COR (Lincoln, Nebr.) LI-190SB quantum sensor and LI-185B meter, 30/20 C day/night air temperature, and 50%/80% relative humidity (RH). Plants were watered frequently and wetted with a dilute nutrient solution once or twice monthly.

The gas exchange system and chamber were identical to that used in MARTIN et al. (1986). Chamber environmental conditions were 1,000–1,800 μmol $m^{-2}s^{-1}$ PPFD (range across chamber interior) for 12 h, 25/20 C day/night air temperatures, and a constant dew point of 15.5 C. A clump of *T. usneoides* was fully soaked, surface-dried, then sealed into the gas exchange chamber on day 0. Each day thereafter the clump was removed, weighed, and resealed in the chamber. During this procedure care was taken to retain small pieces of plant material with the larger clump. At the end of the experiment (day 10), the plants were removed, weighed, dried at 85 C for several days, cooled in a desiccator, and weighed. The experiment was replicated with three different clumps of *T. usneoides*.

FIELD MEASUREMENTS OF TISSUE WATER CONTENT

The study site in the coastal plain of North Carolina and the instruments used for environmental monitoring are described in MARTIN (1980) and MARTIN et al. (1981). Tissue water content was measured by weighing clumps (approximately 5–6 g DW) of *T. usneoides* every 3–4 h over a 24-h period on selected dates from June 1978 to April 1979. At the beginning of a sampling period, five clumps of *T. usneoides* were removed from their host trees and placed with as little compression as possible in nylon mesh bags. The bags were calibrated for weight changes in the laboratory at known atmospheric moisture contents and changes were subtracted from the values of the bagged samples. The bags were hung from twigs and weighed on a portable balance accurate to 0.1 g. After a sampling period, plants were frozen, oven dried (65 C) until no further weight change, cooled in a desiccator, and weighed. Water content (% H_2O) was calculated as

$$\frac{FW - DW}{DW} \times 100.$$

LABORATORY MEASUREMENTS OF TISSUE WATER CONTENT

Clumps of *T. usneoides* were collected from the North Carolina site, transported to the laboratory, placed in different environments, and individually weighed at various intervals on a Mettler top-loading balance accurate to 0.02 g. Clumps were always weighed under the experimental conditions of exposure. Air temperature and RH were measured with a Vaisala HMI12 sensor. Light was provided by 150-W cool-beam floodlamps behind water filters.

WATER VAPOR AND CO_2 EXCHANGE MEASUREMENTS

Plants used in this experiment were collected near Merida, Venezuela, in 1986 and cultivated in the greenhouse of the Institut für Botanik, Darmstadt, under natural lighting conditions, an approximate day/night air temperature of 30/17 C, and a relative humidity of 50%–80%. Prior to measurements, plants were placed for 5 or 10 d in a growth chamber at 300–400 μmol $m^{-2}s^{-1}$ PPFD for 12 h, day/night air temperatures of 20/17 C, and RH of 50%/70%. Plants were not watered during the pretreatment. All gas exchange measurements were made with an infrared gas analyzer (Binos, Leybold-Heraeus, Walz, Effeltrich) equipped with separate columns for detection of both CO_2 and H_2O vapor. The glass gas exchange cuvettes (approximately 9

L) were placed in the growth chamber. Thus, cuvette environmental conditions were the same as those in the growth chamber. Plants were hung inside the cuvettes in their natural orientation. After plotting H_2O and CO_2 exchange curves, the areas bounded by each curve during the day or night only were determined to obtain integrated day and night gas exchange.

Statistical analyses

Since the variability in initial plant water content greatly exceeded the diurnal changes observed in the field and laboratory experiments, the water content means are seldom significantly different when analyzed with analysis of variance (ANOVA). Nonetheless, in each experiment, *all* plants responded in a similar fashion.

The data from the desiccation experiment were analyzed using ANOVA followed by a Student-Newman-Keuls test (SNK) as performed by the SPSS^X (Chicago, Ill.) computer software package. All data were normally distributed without transformation, and means were homoscedastic.

For comparisons with other studies, crude estimates of leaf area-to-weight relationships yielded 4,500 mm^2 = 1 g FW = 0.2 g DW for well-watered plants.

Results

CO_2 exchange during desiccation

Changes in *Tillandsia usneoides* tissue water content were not significant until day 3, after nearly 4 d without water (table 1). Changes in water content were always small, without significant differences between consecutive days. Rates of nocturnal CO_2 uptake were never enhanced by desiccation (fig. 1, table 1), although the total nocturnally assimilated CO_2 did not decrease significantly until day 4. At this point, nocturnal CO_2 accumulation was 65% of the maximum achieved by fully hydrated specimens (fig. 1, table 1).

Changes in tissue water content

Diurnal patterns of changes in *T. usneoides* plant water content were similar at all times of year except during rains, when the experimental plants were sheltered. The typical pattern consisted of nocturnal water vapor uptake followed by daytime water loss (fig. 2). Plant water content always tracked atmospheric RH. Although nocturnal RH was always high at this study site in North Carolina, the plants never appeared physically wet, as by dew deposition. Furthermore, on all nights excepting those with rain, RH never approached 100% throughout most of the night when plants absorbed water vapor. The amount of water absorbed from the atmosphere at night was always, with the exception of high daytime RH during a rain, less than the amount of water lost the next day (table 2). Thus, between rainfall events, plants became drier each day (fig. 3).

Similar patterns of changing plant water content were observed under controlled conditions in the laboratory where plants tracked atmospheric RH (fig. 4*a*). Plants kept at 50% RH throughout a 24-h period exhibited continual, slow rates of water loss (fig. 4*b*), whereas those kept at 86% RH without light showed little change in plant water content (fig. 4*c*). In addition, the water content of heat-killed plants also tracked changes in environmental RH (table 3). Finally, as indicated for plants in the field, nocturnal water vapor uptake did not offset daytime losses under laboratory conditions. At any specific time of day or night plant water content decreased day to day (fig. 5).

TABLE 1

Mean (±SD) water content and total nighttime CO_2 uptake in Tillandsia usneoides sealed in a gas exchange chamber for 10 d

Days without water	Water content % of DW		Integrated night CO_2 uptake mmol g^{-1} DW	
0	362 ± 16	a	.20 ± .03	a
1	340 ± 15	ab	.19 ± .05	ab
2	322 ± 14	ac	.16 ± .02	abc
3	308 ± 15	bcd	.14 ± .02	abcd
4	295 ± 16	cde	.13 ± .04	bcd
5	284 ± 17	cdef	.11 ± .02	cd
6	274 ± 17	defg	.10 ± .01	cd
7	264 ± 17	efg	.09 ± .02	cd
8	255 ± 16	fg	.08 ± .02	cd
9	247 ± 17	g	.07 ± .02	d

Note.—Means with the same letter are not significantly different ($P > 0.05$) by SNK. No. = 3.

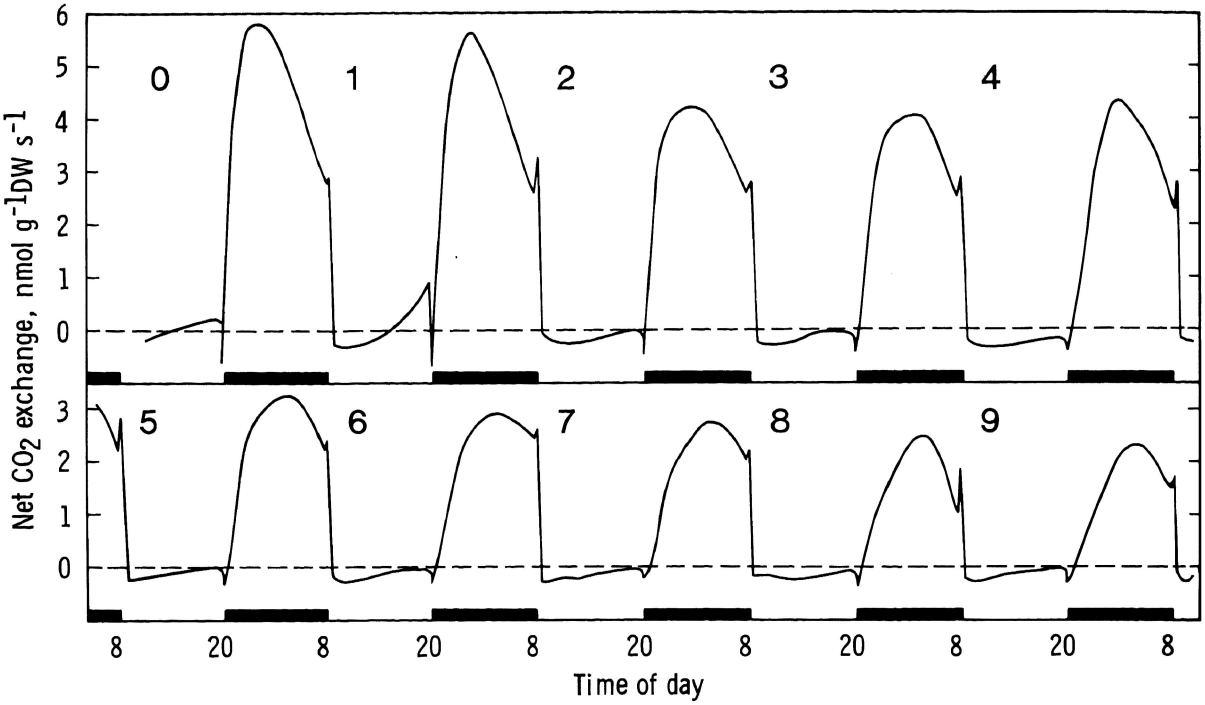

FIG. 1.—Effects of decreasing tissue water content on net CO_2 exchange in *Tillandsia usneoides* for 9 continuous d following wetting of the tissue on day 0. Black bars indicate darkness. Curves are means of three clumps; coefficients of variation were ca. 30%. Environmental conditions are given in Material and methods.

CO_2 AND H_2O GAS EXCHANGE

At humidities well below saturation, plants of *T. usneoides* exhibited water vapor uptake immediately after lights-out when CO_2 uptake commenced, followed by low rates of H_2O loss throughout the remainder of the night (fig. 6). Upon illumination, a burst of water loss from the plants was followed by additional efflux throughout the day. Water loss always exceeded uptake (table 4). Although the data are limited, a longer period without water decreased water vapor loss while enhancing nocturnal water vapor uptake.

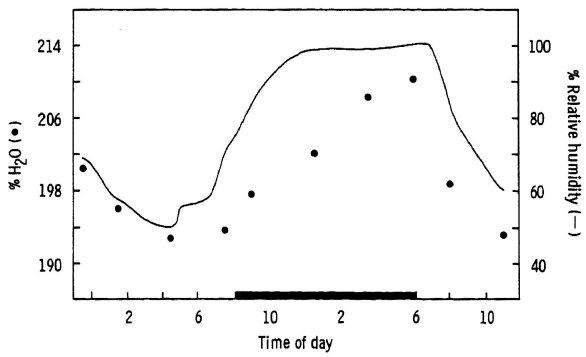

FIG. 2.—Mean changes in tissue water content (dark circles) throughout June 24–25, 1978, in situ in North Carolina for five clumps of *Tillandsia usneoides*. Coefficients of variation were ca. 10%. The continuous line denotes atmospheric RH. Black bar indicates darkness.

Discussion

Drought stress did not enhance nocturnal CO_2 uptake in *Tillandsia usneoides* as has been suggested in the past (KLUGE et al. 1973; MARTIN et al. 1981; MARTIN and SIEDOW 1981). Although tissue water content and, hence, nocturnal CO_2 uptake declined very slowly, this atmospheric epiphyte responded to increasing tissue desiccation as do terrestrial CAM plants, i.e., by reducing CO_2 uptake (SZAREK and TING 1975; KLUGE and TING 1978). The lack of a positive correlation between nocturnal CO_2 uptake and tissue water content reported by MARTIN et al. (1981) is difficult to interpret since too many environmental conditions as well as plant water content varied between sampling dates in the field. KLUGE et al. (1973) used two different groups of plants in their study of the effects of different water contents on nocturnal CO_2 uptake; a third group was also monitored for gas exchange in this experiment, yet it was wet during the measurements. The differences they observed were very small and may have reflected plant-to-plant variability. Finally, the reduction in CO_2 uptake following wetting and drying of the same clump of *T. usneoides* noted by MARTIN and SIEDOW (1981) may have resulted from inadequate drying of the

TABLE 2

MEAN (±SD) NET 24-H CHANGES IN WEIGHT: NET UPTAKE (positive value) OR LOSS (negative values) OF WATER BY FIVE CLUMPS OF TILLANDSIA USNEOIDES IN SITU IN NORTH CAROLINA

Dates	Net 24-h weight change mg g^{-1} DW
June 24–25, 1978	−74 ± 24
August 1–2, 1978	−46 ± 16
August 21–22, 1978	−66 ± 10
September 9–10, 1978	−16 ± 10
September 30–October 1, 1978	+70[a] ± 23
October 21–22, 1978	−18 ± 16
November 11–12, 1978	−165 ± 59
December 2–3, 1978	−31 ± 24
December 17–18, 1978	−30 ± 17
March 31–April 1, 1979	−74 ± 9
April 20–21, 1979	−26 ± 2

NOTE.—Environmental conditions on each date can be found in MARTIN (1980).

[a] Raining during day; plants protected from rain.

tissue, since surface water reduces rates of gas exchange in this plant (BENZING and RENFROW 1971; MARTIN et al. 1981; MARTIN and SIEDOW 1981).

This study clearly shows that *T. usneoides* is capable of absorbing water vapor at night, as indicated by PENFOUND and DEILER (1947) and VIRZO DE SANTO et al. (1976). Although this unusual phenomenon undoubtedly prevents or limits tissue water loss at night, it does not prevent net water loss on a 24-h basis.

Since the water content of dead plants also tracked changes in atmospheric RH, it is apparent that water vapor absorption is a physical phenomenon, unrelated to the metabolic state of the plant. This water vapor exchange is most likely mediated by the trichomes densely covering the leaves of atmospheric epiphytes (BENZING and BURT 1970; BENZING et al. 1978). These are large, multicellular hairs with living "stalk" cells and dead "shield" cells (BILLINGS 1904; MEZ 1904; SCHULZ 1930; BENZING 1976; BENZING et al. 1976). Of especial interest regarding the current study are the outermost walls of the shield cells. These walls are extremely thick and reportedly very rich in pectin—a hygroscopic polysaccharide (MEZ 1904). VIRZO DE SANTO et al. (1976) proposed that the observed water vapor exchange reflects the hydration and dehydration of these trichomes.

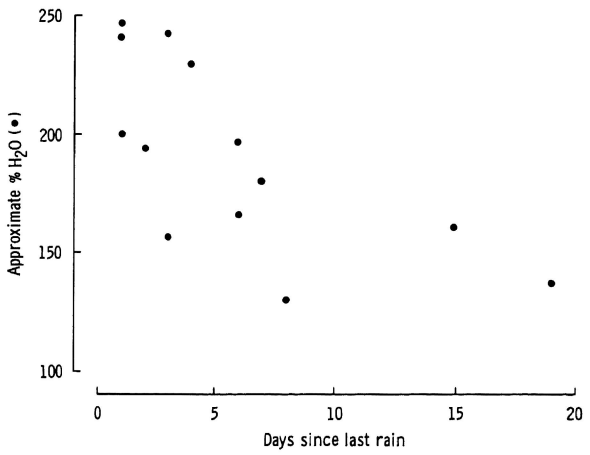

FIG. 3.—Means of approximate tissue water content after varying lengths of drought in situ in North Carolina for *Tillandsia usneoides*. Values were calculated by averaging mean water contents of five clumps at all times for each sampling period.

Two "pools" of water apparently exist in *T. usneoides* which are coupled, directly or indirectly, with the atmosphere: the water constituting the bulk of the living mesophyll cells, and the water held matrically in the nonliving trichomes. Exchange of water with the atmosphere by these two pools is controlled by different mechanisms. Since the two pools are linked by the trichome basal cells which are living (BENZING 1976), water exchange between both is likely. Such exchange, however, is likely to be very slow, relative to exchange with the atmosphere, given the probable differences in resistances to water movement.

Water exchange between the trichomes and the atmosphere is passive, dependent simply on the prevailing atmospheric humidity. In contrast, since CO_2 exchange in *T. usneoides* and at least one other atmospheric epiphyte is under stomatal control (LANGE and MEDINA 1979; MARTIN and SIEDOW 1981; MARTIN and PETERS 1984), water vapor exchange by the mesophyll cells of this epiphyte must also be controlled by the stomata. Although the water potential of these living cells is unknown, it

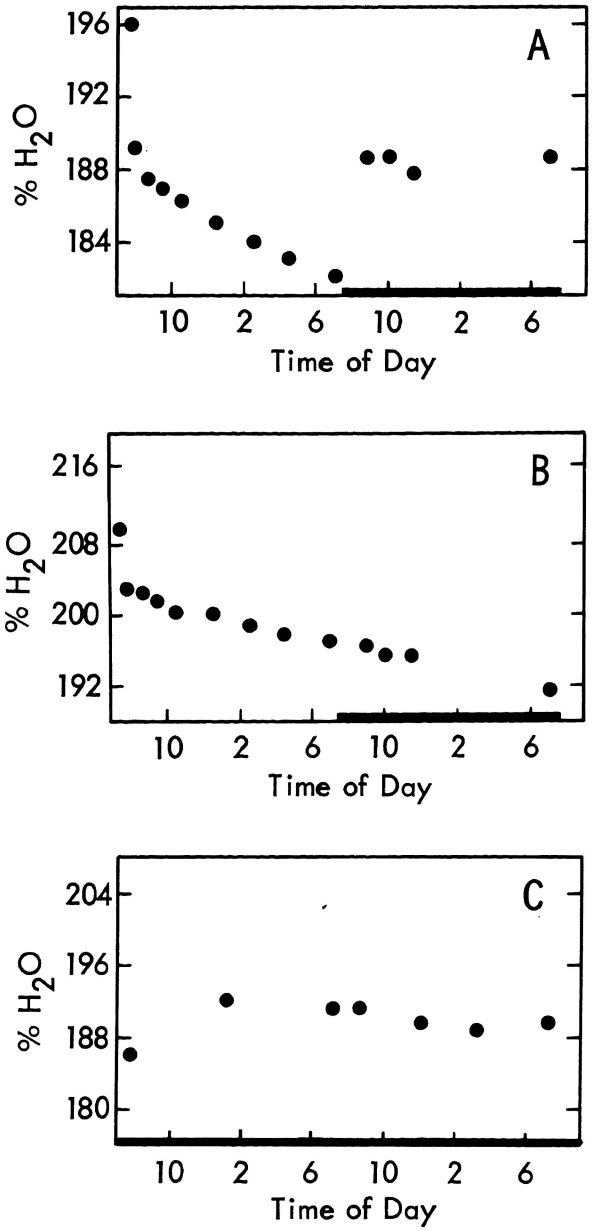

FIG. 4.—Mean changes in tissue water content under controlled conditions in the laboratory for five clumps of *Tillandsia usneoides*. Coefficients of variation were ca. 5%. Black bars indicate darkness. Environmental conditions were (*A*) 30 C, 50% RH day and 30 C, 90% RH night; (*B*) both day and night at 30 C, 50% RH; and (*C*) constant darkness, 15 C, 86% RH.

should be much higher than that of the surrounding air, except under conditions of saturating vapor pressure. Thus, except during brief periods of 100% RH (some, but not all, days at the site in North Carolina), water should always be lost by the living cells to the atmosphere, or to the trichome shields.

The potential simultaneous interactions of these

TABLE 3

MEAN (±SD) WATER CONTENT OF HEAT-KILLED (60 C for 4 d) TILLANDSIA USNEOIDES BEFORE, DURING, AND AFTER AN INCREASE IN ATMOSPHERIC RH

Treatment	Water content % H_2O
50% RH, 30 C.....	3.5 ± 0.5
90% RH, 15 C.....	11.3 ± 0.7
50% RH, 30 C.....	4.3 ± 0.3

NOTE.—Values are means of 10 plants. % H_2O is on a DW basis.

two pools of water with the atmosphere and between themselves complicate interpretation of the water relations of this, and perhaps all, atmospheric epiphytes. At this time, the following scenario appears most likely. Early in the night, when stomata open and whole-plant water vapor uptake occurs, the trichomes, dried during the preceding day, must begin to absorb water from the cooler atmosphere as well as from the living cells "below," via the stomata (BILLINGS 1904; MARTIN et al. 1985). Since atmospheric humidity typically increases throughout the night in the field (see fig. 2), this process should continue all night. Under experimentally manipulated conditions, e.g., constant RH at night, transpiration is observed (fig. 6) since the water content of the trichomes is presumably at equilibrium with the atmospheric water content. Thus, during this time, calculated water-use efficiencies are typical for CAM plants (table 4).

The possibility exists, under conditions of atmospheric water vapor saturation (which may also cause dew condensation), that the normal atmosphere-to-living cells water potential gradient is reversed and water vapor hydrates the living cells. But, under nonsaturating conditions, it should be

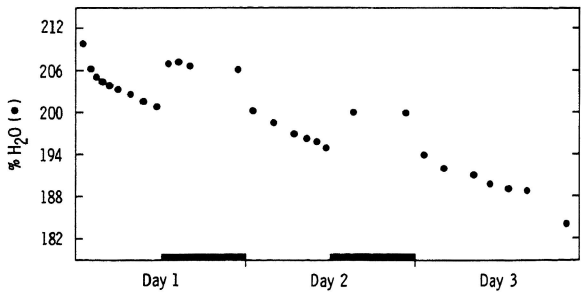

FIG. 5.—Mean changes in tissue water content during 3 continuous d under controlled conditions in the laboratory for five clumps of *Tillandsia usneoides*. Coefficients of variation were ca. 5%. Black bars indicate darkness. Environmental conditions were 30 C, 50% RH day and 30 C, 90% RH night.

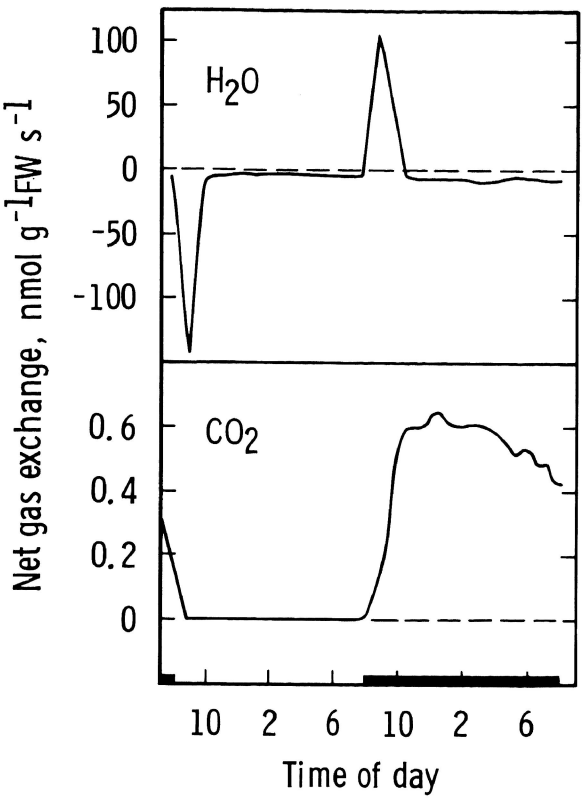

FIG. 6.—Net 24-h CO_2 and H_2O vapor exchange in one large clump (ca. 15 g FW) of *Tillandsia usneoides*. Positive values indicate gas uptake; negative values indicate gas loss. Two other clumps exhibited identical patterns of gas exchange, though actual rates varied substantially. Environmental conditions are given in Material and methods. Black bar indicates darkness.

emphasized that the living cells should continue to lose water to the trichomes throughout the night, even if the whole plant continues to exhibit water vapor uptake.

Upon illumination, large amounts of water are lost by the whole plant. It is likely that such water originates mainly from the trichome pool, since the stomata are closed or closing at this time (MARTIN and PETERS 1984). As atmospheric relative humidity decreases throughout the day, all, or nearly all, water should continue to be lost from the trichomes. Since daytime water losses typically exceed nighttime uptake (table 2), not only is all the water previously absorbed at night lost, but water must also be lost from the mesophyll cell pool. Since daytime CO_2 losses are relatively small, the stomata of *T. usneoides* appear to be tightly closed. Thus, it is hypothesized that water is lost from the living cells through the trichomes themselves. If true, the trichomes are not as efficient at preventing water loss as was previously thought (MEZ 1904). Nonetheless, daytime stomatal closure in this species prevents further daytime water loss as in other CAM plants (KLUGE and TING 1978).

The trichomes of atmospheric epiphytes may retard water loss by increasing the thickness of the boundary layer (but see JOHNSON 1975). On the other hand, they appear the most likely conduits for slow rates of water loss observed throughout the day. If the trichomes and the water vapor exchange associated with them are ignored, it is apparent that the water relations of these epiphytic CAM plants are not unlike the water relations of their terrestrial counterparts.

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TABLE 4

MEAN INTEGRATED (24 h) WATER UPTAKE, LOSS, AND NET EXCHANGE FOR THREE CLUMPS OF TILLANDSIA USNEOIDES

Clump no.	H_2O vapor uptake mg g^{-1} FW d^{-1}	H_2O vapor loss mg g^{-1} FW d^{-1}	Net H_2O vapor exchange mg g^{-1} FW d^{-1}	Mid-night water use efficiency (μmol CO_2 g^{-1} FW d^{-1}) / (μmol H_2O g^{-1} FW d^{-1})
1	14.1	50.4	−36.2	0.045
2	17.5	25.6	−8.1	0.100
3	16.3	27.8	−11.4	0.060

NOTE.—Negative values indicate net H_2O vapor loss. Values were obtained from fig. 6. Clump 1 was not watered 5 d before measurements; clumps 2 and 3 received no water for 10 d.

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