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Autor(en): **Eller, Benno M. / Ruess, Béatrice R. / Ferrari, Sandro**

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Reestablishment of water uptake by succulents after drought: Potometric field determinations in the Richtersveld (Cp., Rep. South Africa)

Benno M. Eller, Béatrice R. Ruess and Sandro Ferrari

Institut für Pflanzenbiologie, Universität Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland

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Abstract

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Transpiration and water uptake by the roots of two succulents – *Othonna opima* D.C. and *Mesembryanthemum pellitum* Friedr. – were measured in the Richtersveld (southern Namib desert) with a potometric system. The drought stressed plants reacted to the reestablished water supply by a high transpiration within 24 hours of the transfer to the potometer. *O. opima* and *M. pellitum* showed a high water uptake rate after 3 and 5 hours, respectively. This proved that these succulents react quickly to a reestablished water availability from the soil to refill their water storage tissues.

Key words: Crassulacean acid metabolism (CAM), drought stress, potometer, transpiration, water uptake.

Introduction

During extended periods of insufficient rainfall, succulent plants progressively lose their stored water reserves and complete desiccation can occur if the drought persists. In the Richtersveld (Southern Namib desert), 50% of the evergreen succulents with crassulacean acid metabolism (CAM) were damaged during the dry period from 1977 to 1980 (von Willert and Brinckmann 1986). After a rainfall the water content of the soil is within a short time strongly reduced by the high evaporative demand of the dry air. Evaporation from the soil is further increased during the so called bergwind conditions (period with hot winds falling down the escarpment of the Namib desert) which are in the Richtersveld very frequent during the rainy season (von Willert et al. 1991). For succulents in such habitats it is essential to reestablish water uptake by the roots very quickly to make use of the soil moisture in order to refill their water storage tissues. The more the water stores can be refilled after a short rain the longer a subsequent drought period can be endured by succulents.

In cacti, Kausch (1965) showed that the absorbing roots are formed a few hours after reestablished water supply and that a high transpiration rate was reestablished within a day. In *Agave americana* and *Ferocactus acanthodes*, Nobel (1976, 1977) reported an almost maximal stomatal aperture 48 hours after rainfall as the consequence of an already improved water status of the plants through water uptake from the soil. However, direct measurements of water uptake after drought were hitherto restricted to the laboratory (Ruess and Eller 1985). They have shown that *Senecio medley-woodii* reacts to the reestablished water supply with a high rate of water uptake within 2 hours after the transfer to a potometer. A first use of the potometric technique in the field, in order to evaluate the water budget (water uptake minus transpiration, for the given time) of succulents was made by Ruess et al. (1988) in the natural habitat of succulents in the province Transvaal in South Africa. These measurements were made during the rainy season and in this study the aim was to quantify the water budget of drought stressed succulents reacting upon improved water availability. The presented results must be considered as a first quantification of the time that elapses until leaf succulents in the Richtersveld have reestablished water uptake and transpiration.

Material and methods

The study was undertaken in the Richtersveld (Southern Namib desert, Republic of South Africa) near the old copper mine at Numees, during February 1987. Informations on vegetation and climate of this area are given by von Willert et al. (1980, 1985). Measurements were made with *Othonna opima* D.C. (Asteraceae) and *Mesembryanthemum pellitum* Friedr. (Mesembryanthemaceae). *Othonna opima*, an evergreen succulent with upright cylindrical leaves is regarded to be a C₃-succulent (von Willert et al. 1984). *Mesembryanthemum pellitum* is an annual succulent having the idioblast type of epidermis (Ihlenfeldt and Hartmann 1982) and is a CAM-succulent. At the time of the investigations, the soil in the habitat was very dry (soil water potential below 3 MPa).

Measurements were made using a weighing potometer as described by Ruess et al. (1988). Hourly weighing of the whole equipment were made with an electronic balance (Mettler, PL 1200-02, Greifensee, CH). A loss of weight must be interpreted either as transpirational water loss of the plant and/or evaporation from the plant or the potometer itself. An increase of weight occurs if dew is formed on the plant or the potometer or water uptake by hygroscopy. From laboratory measurements we know that hygroscopic water uptake or release by the surfaces of the potometer are usually very small and can be neglected. Water uptake by the roots of the plant was determined by measuring the volumetric variation of the water in the container in which the root system of the plant bathed. To avoid an excessive heating of the water in the potometer by absorbed solar radiation, the water containers were covered with aluminium foil. Only small plants could be used as a consequence of the dimensions of the potometer. For an evaluation of the transpiration rate of the drought stressed plants, plants similar to those used with the potometer were taken. Their roots were cut off, the cut sealed with vaseline and the plants exposed to environmental conditions. Weighing of the plants were then made every hour with a balance (Mettler, AE 163, Greifensee, CH).

Nocturnal dew formation was estimated (every hour) using dew gauges consisting of unglazed porcelain discs (Diameter: 110 mm, thickness: 5.5 mm (Steubing 1952)). True air temperature and relative air humidity were determined with an aspirated psychrometer (Hänny, Jegenstorf, CH) and solar irradiance with a solarimeter CM5 (Kipp & Zonen, Delft, NL). Leaves of the plants were killed by immersing in boiling water for 10 minutes. The leaves then were crushed and the osmolality of the sap was determined with an osmometer (Mod. 3 B, Vogel, Giessen, BRD). The leaf samples then were dried at 90 °C. Transpiration and water uptake rates were calculated per unit dry weight (DW). Malate amount was determined enzymatically after Möllering (1974) in the laboratory at Zürich, in aliquots of hot-water extract of the dried leaves.

Results and discussion

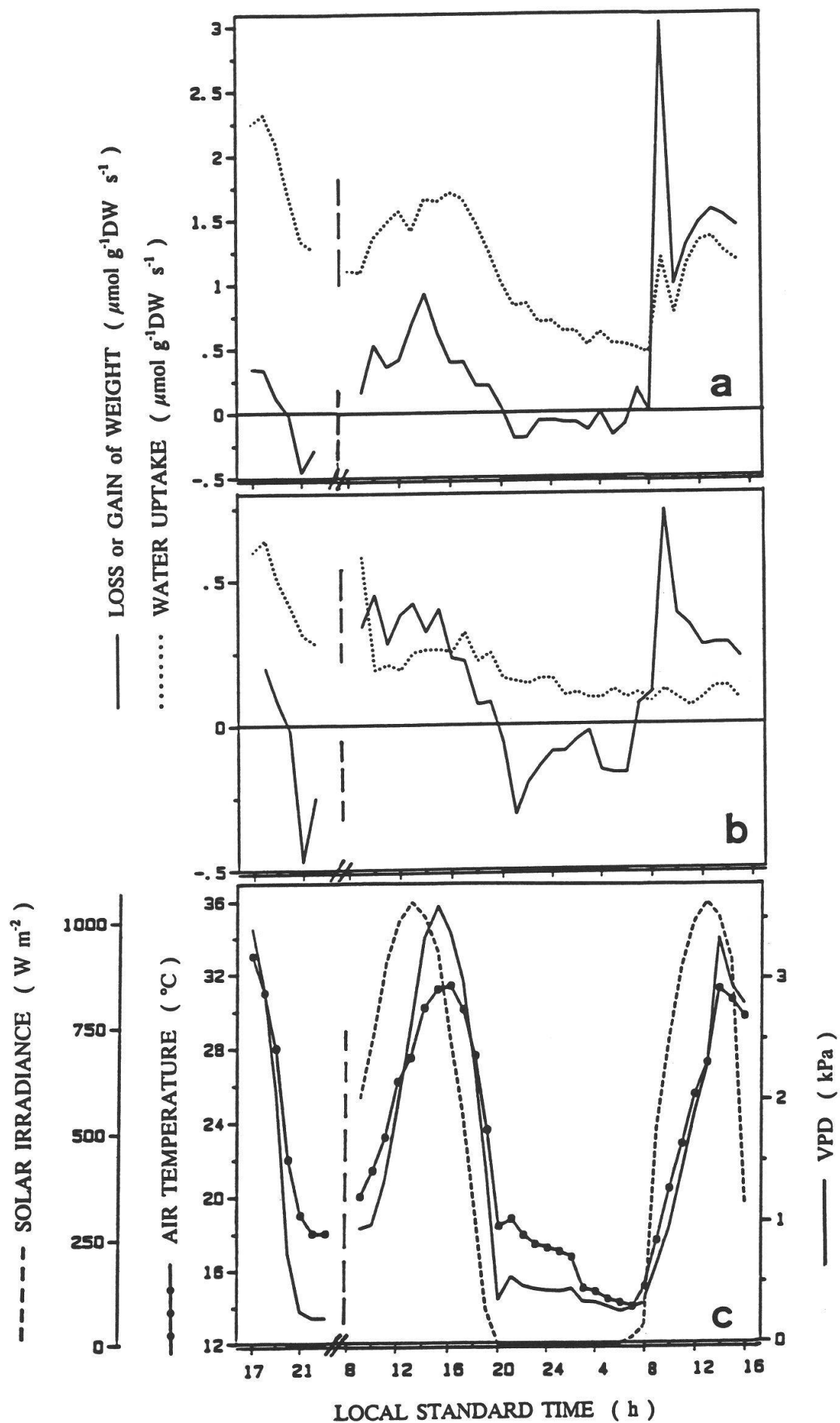
The highest and the lowest air temperature during the measurements were 31.4 °C and 14 °C, respectively (Fig. 1 c). The water vapour pressure deficit (VPD) of the air varied between 3.6 and 0.2 kPa. From about 03h00 to 07h00 dewfall was visible on the potometer. The total amount of dew was 0.03 mm (Fig. 2). This dew formation resulted an increase in the weight of the potometer (including the plant) measured between 03h00 and 07h00 (Fig. 1). The peak registered at beginning of the day was mainly caused by evaporation of the dew (Fig. 1). However, with *Othonna opima* (Fig. 1 a) at the same time a much smaller peak was also visible for water uptake which might indicate that this plant transpired and by this had lowered its water potential which caused an increase of water uptake.

Three hours after the transfer of *O. opima* to the potometer (Fig. 1 a first day, at about 18 h), a high water uptake rate of 2.3 $\mu\text{mol g}^{-1} \text{ DW s}^{-1}$, exceeding 7 times the water loss by transpiration, could be observed (Fig. 1 a). On the second day, the water uptake was still higher than the transpirational water loss and a positive water budget (water uptake minus transpiration) of 66.3 $\text{mmol g}^{-1} \text{ DW}$ over the 24 h period resulted. As a consequence of this significant water gain, the transpiration on the third day of measurements (Fig. 1 a, from about 09h00) was even higher than the water uptake, indicating that the water deficit of the plant was already substantially reduced. At about 13 h the transpiration rate was 1.57 $\mu\text{mol g}^{-1} \text{ DW s}^{-1}$, this in contrast with the value obtained from the measurements of the transpiration of a similar plant kept under drought (0.19 $\mu\text{mol g}^{-1} \text{ DW s}^{-1}$, Fig. 3 a).

A similar reaction to the reestablished water supply could be monitored with *M. pellitum* (Fig. 1 b). A higher water uptake rate was measured within 5 hours after the transfer to the potometer. It is assumed that the water deficit of this plant was smaller than the one of *O. opima*. Indeed transpirational water loss exceeded water uptake on the second day (Fig. 1 b, from 08h00 to 18h00). The resulting positive water budget over 24 h was 3.8 $\text{mmol g}^{-1} \text{ DW}$. The transpiration rate on the second day reached 0.45 $\mu\text{mol g}^{-1} \text{ DW s}^{-1}$ while it was 0.13 $\mu\text{mol g}^{-1} \text{ DW s}^{-1}$ for the drought stressed plant (Fig. 3 b).

The positive water budget of *O. opima* on the second day was 66.3 $\text{mmol g}^{-1} \text{ DW}$ while it reached only 3.8 $\text{mmol g}^{-1} \text{ DW}$ for *M. pellitum*. This difference results partly from the high salt concentrations of *M. pellitum* which contribute substantially to the dry weight of this plants, as was measured by von Willert et al. (1980).

Other data from our experiments indicate that the water deficit of *M. pellitum* is less prominent than that of *O. opima*. The high daytime transpiration of the drought stressed plant (Fig. 3 b) reaching 0.13 $\mu\text{mol g}^{-1} \text{ DW s}^{-1}$ can be considered as a further indication of the fairly good water status of *M. pellitum*. The corresponding value after remoistening was 0.36 $\mu\text{mol g}^{-1} \text{ DW s}^{-1}$ (Fig. 1 b, mean of the highest values at the second day). One reason for this could be the ability of *M. pellitum* to recuperate water from older leaves which dry progressively from the leaf tip towards the leaf base (von Willert et al. 1980). Such partially dried leaves tips could be observed at the plants used for the measurements. Another reason for a better water status of *M. pellitum* compared with *O. opima* could be the absorption of water vapour from the air by parts of the plant above soil level. In Fig. 1, both plants (more precisely the potometer with the plant fixed in it) showed an increase in the weight of the potometer between 20h00 and 03h00, although no dew-fall occurred during this time period (Fig. 2). However, the increase by *O. opima* was small and could have been caused by hygroscopic uptake of water vapour



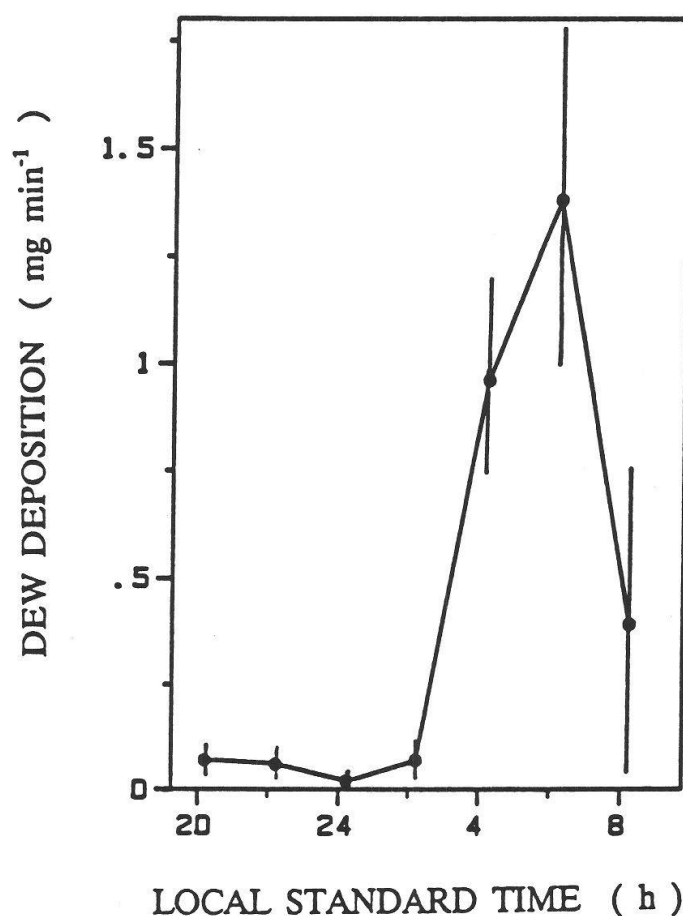


Fig. 2. Formation of dew during the experiment as determined using the dew gauges of Steubing (1952).

by the plant surfaces or, to a small amount, by the potometric equipment. In contrast, the increase in the weight of the potometer of *M. pellitum* was clearly more pronounced and could be an indication of true uptake of water vapour from the air. This supposition is also valid for the same time period of data measured with the drought stressed plant (Fig. 3b). The conditions necessary for such a "reversed transpiration" in plants of the Namib desert have been discussed by von Willert et al. (1985). One prerequisite is a rather high osmolality of the cell sap. We measured for *M. pellitum* at dawn and at dusk 1.62 and 1.55 osmol, respectively. The plants of *M. pellitum* exhibited CAM with a nighttime accumulation of malic acid of 75 mol m^{-3} . We must suppose that the high osmotic potential together with its further increase by malate accumulation during night contributes to establish a water vapour gradient from the atmosphere into the leaf, which is the fundamental prerequisite for nocturnal uptake of water vapour from the air.

Fig. 1. Water relations for *Othonna opima* (a) and *Mesembryanthemum pellitum* (b) measured with a weighing potometer during a three day period (first day 17h00–21h00, second day 08h00–24h00, third day 00h00–16h00). c: Environmental conditions for the same timespans.

Water uptake: Uptake by the roots (volumetric determination). Loss of weight (positive values): Transpirational water loss by the plant or evaporation of dew or hygroscopic water. Gain of weight (negative values): Deposition of dew or uptake (hygroscopically) of air humidity by the surfaces of the plant or the potometer. DW = Dry weight of plant.

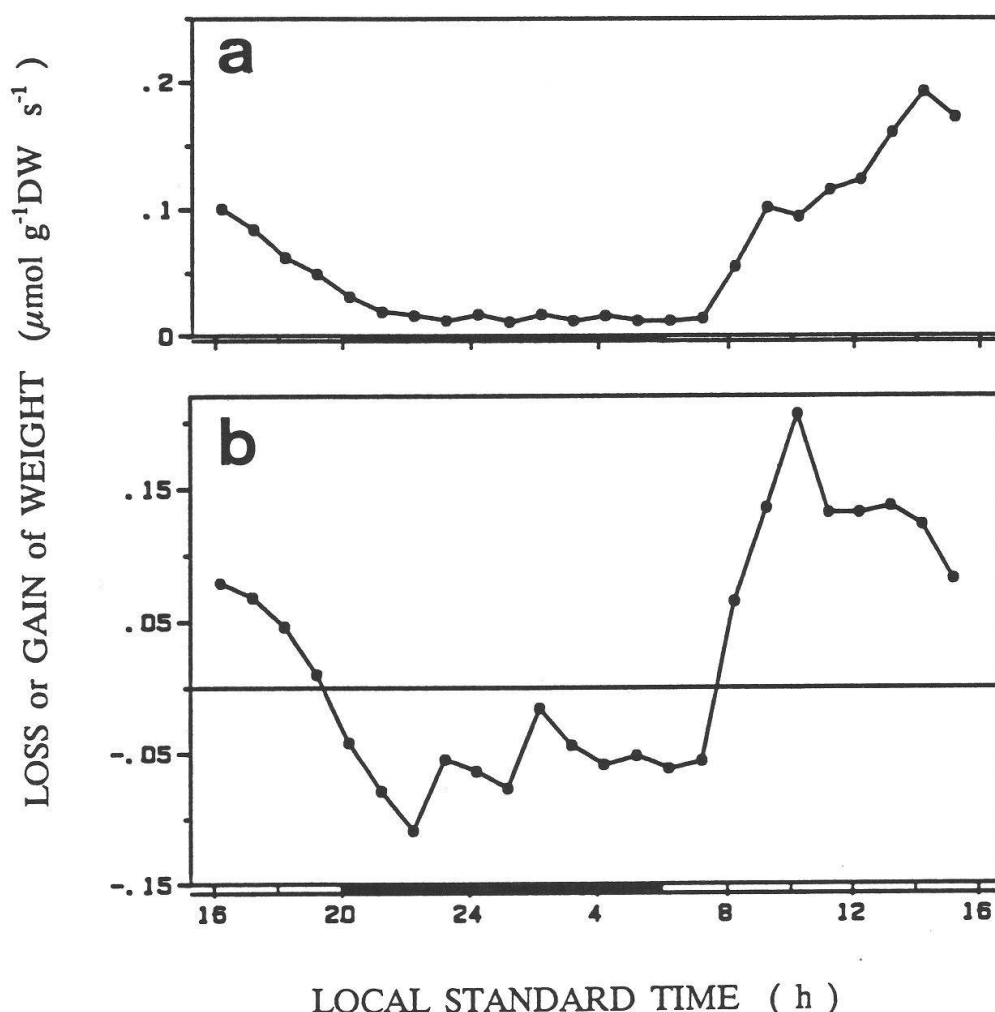


Fig. 3. Loss or gain of weight of excised branches of *Othonna opima* (a) and *Mesembryanthemum pellitum* (b).

Loss of weight (positive values): Transpirational water loss by the plant and/or evaporation of dew or hygroscopic water of the plant surfaces. Gain of weight (negative values): Dew deposition on the plant surfaces and/or water vapour uptake by the plant either through "reversed transpiration" or hygroscopically. DW=Dry weight of plant. Environmental conditions as in Fig. 1. (second and third day).

Conclusions

The results show that after a prolonged drought *O. opima* and *M. pellitum* were able to reestablish a high water uptake within 3 and 5 hours, respectively. This supports the findings of Nobel and Sanderson (1984) that rehydration of existing roots is primarily responsible for the substantial uptake of water after the first hours of rewetting. However, the development of new roots by *Opuntia puberula* was observed within 8 hours after reestablishment of water supply (Kausch 1965). The potometric system used during this study allowed an estimation how quick drought stressed succulents are able to collect water in their natural environment after rainfall and allow plants to spend more water through transpiration following an increase of stomatal conductivity to enhance CO_2 gain. With *O. opima*, the water uptake rate after the transfer to the potometer was

12 times higher than the transpiration rate of an equivalent drought stressed plant. Furthermore, a high transpiration was measured within 24 hours after the transfer to the potometer, demonstrating that the plant water status was markedly improved.

We consider our results a first attempt to make field estimations of the capacity of droughted plants to react on reestablished water availability from the soil. The potometric method could be suitable to study a possible uptake of water vapour from the air or to quantify the very often assumed contribution of fog or dew to the water economy of succulents in desert habitats like the Namib. However, some improvements of the equipment in order to reduce uptake and release of water vapour by the surfaces of the potometer and prevention of dew deposition on this surfaces (but not necessarily on the plant surfaces) have to be made.

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