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Welwitschia mirabilis: Observations on movement of water and assimilates under föhn and fog conditions

by
Chris H. Bornman, C. E. J. Botha and Linda J. Nash
Department of Botany, University of Natal, Pietermaritzburg
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ABSTRACT

Evidence that *Welwitschia* is able to absorb and translocate the water which condenses on its leaves under foggy conditions has been obtained by the application and subsequent localisation of tritiated water. Scanning electron microscopy of the leaves suggests that the path of water uptake may be via the stomata. Rates of uptake under foggy and föhn wind conditions are compared. Preliminary investigation of the movement of photosynthetic assimilates indicates that these are rapidly translocated in the direction of the meristematic regions.

INTRODUCTION

Welwitschia mirabilis is, as has been described elsewhere (Bornman, Elsworthy, Butler and Botha, 1972), a plant of strikingly bizarre habit and one which may successfully survive the extremely arid conditions of the northern Namib Desert for up to two thousand years. The water relations of *Welwitschia* are thus of great interest. Although the large colony studied on the so-called Welwitschia Flats east of Swakopmund is established in sand superficially devoid of moisture and the relative atmospheric humidity of the area may drop to zero (Table 1), dense advection fogs nevertheless occur over the flats. Under these conditions appreciable amounts of water condense on the leaves, whose vast surface area and specialised internal anatomy suggest that this may be the means whereby the plant's water requirements are met.

In this study, water uptake, translocation and transpiration by the leaves were investigated in the field by applying tritiated water both to intact leaf surfaces and internally to the leaf meristem. It was possible to obtain comparable data under the two extreme weather conditions experienced on successive days: namely, fog and föhn wind (Table 2). In addition, the photosynthetic activity of mature leaves and the rate of translocation of photosynthates were estimated by supplying $^{14}CO_2$ to the adaxial surface of a leaf.

MATERIALS AND METHODS

Scanning electron microscopy

Pieces of stem and leaf from both abaxial and adaxial surfaces, 25 mm^2, were freeze-dried, lightly coated with gold-palladium, and viewed in a Hitachi SSM-2 scanning electron microscope.

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Tritiated water

Stock solutions with a specific activity of 6,0 x 10^5 dpm per ml were prepared by diluting tritiated water (Radiochemical Centre, Amersham, England) with sterile glass-distilled water and ethanol, 95:5 v/v. A suitable plant was selected in our experimental area on the Welwitschia Flats and four 4,5 cm-deep holes bored in the meristematic zone of stem tissue on the adaxial side of the stem groove. A Pasteur pipette was inserted in each of the holes. Liquid-scintillation vials were taped to the adaxial surface of the leaf, in line with the pipettes (Fig. 5) and 1,0 ml of stock solution was added to each pipette, the open ends of which were then plugged with cotton wool. After 4, 7, 10 and 24 hours, vials were removed and carefully capped.

On the opposite leaf, a vaseline trough was made and irrigated with 2,0 ml tritiated water, and the trough sealed with plastic film to prevent evaporation. After 2, 3, 7 and 10 hours, 1 cm^2 pieces of leaf tissue were cut at predetermined distances from the trough, 8 in a proximal direction and 2 in a distal direction. Each square was placed in a scintillation vial containing 2 ml absolute ethanol. A similar experiment was conducted on day 2 with sampling periods of 0,5 and 1,0 hour respectively.

$Ba^{14}CO_3$

A $Ba^{14}CO_3$ stock (Radiochemical Centre, Amersham) was mixed with unlabelled barium carbonate in the ratio 1:5 for a specific activity of 3,5 x 10 dpm/mg. Five-milliliter test tubes were attached to wooden dowels which were positioned in the sand in such a way that good contact was made between the lip of the tube and the abaxial leaf surface, about 10 cm from the stem. The lip was lightly greased to ensure sealing. A drop of concentrated H_2SO_4 was added down the side of each test tube and it was quickly sealed into position against the leaf surface. Leaves were exposed for 5, 10 and 20 minutes respectively to the evolving $^{14}CO_2$, after which a strip of 1 x 5 cm, measured from the meristem was cut into five 1-cm squares, each of which was placed in a vial containing 2 ml absolute ethanol. An increment borer was used to obtain tissue from the meristematic zone, 2-cm cylinders of which were placed in vials as above.

Liquid-scintillation counting

After 1 week, the leaf squares and meristem bores were transferred to vials containing 15,0 ml of the following scintillation fluid; naphthalene 60 g, PPO 4 g, dimethylPOPOP 200 mg, absolute ethanol 125 ml, ethylene glycol 20 ml, toluene to 1 litre. Since chlorophyll was still present in the samples, a channels-ratio method of counting was used to correct for non-uniform quenching. Suitable ratios were determined with prepared quenched ^3H- and ^{14}C-standards (Radiochemical Centre, Amersham). Counting efficiency and channels ratios for these standards were calculated to an error of not more than 0,001% using an Olivetti P-101 desk-top computer. The resulting values were plotted as x, y coordinates and the complete function (channels-ratio vs. % counting efficiency) calculated by computer (IBM 1130) and tabulated at intervals of 0,001 unit. These functions were used to calculate absolute dpm values for each sample. All samples were then counted for ^3H and ^{14}C radioactivity in a Nuclear-Chicago Unilux II liquid-scintillation spectrophotometer.

RESULTS

1. Movement of tritiated water

Figure 6 shows that the tritiated water was rapidly taken up from the Pasteur pipettes placed at the stem-leaf interface, and was translocated along the leaf away from the point of application. In spite of the artifically-created microclimate under the vials taped to the upper epidermis (Fig. 5), this translocated water was transpired and collected in the vials in easily-detectable amounts. The amount of water trapped was generally found to increase with increasing distance from the point of application (Fig. 6), except in the 24-hour experiment where this trend was reversed. As is clearly demonstrated in Fig. 7, an intact *Welwitschia* leaf will take up water from an external source even under foehn wind conditions, and this water is made available to all parts of the leaf by translocation.

The most striking feature of the results illustrated in Fig. 7 is the comparison between proximal and distal diffusion rates. It is evident that most of the water taken up by the leaf was translocated in a proximal direction, away from the point of application, and thus towards the actively-meristematic stem regions. Furthermore, Fig. 7 indicates that distal translocation is minimal by comparison with proximal. Between 3 and 7 hours, distal translocation increased, however, a trend which may be correlated with a 40° C drop in recorded air temperature between hour 2 and hour 7 of the experiment.

Sharply-differing results were obtained from experiments conducted the following day under fog conditions (Fig. 8). These results indicate that translocation of tritiated water applied directly to the adaxial leaf surface tends to proceed in both directions away from the point of application. Nevertheless, proximal translocation is inferred to be a far more rapid phenomenon than the corresponding distal movement, since the values recorded for distal translocation are initially higher than the corresponding proximal values but decrease rapidly away from the application point, whereas proximal translocation of tritiated water is relatively constant.

2. $^{14}CO_2$ assimilation

As is shown by Figs. 9, 10 and 11, and Table 2, $^{14}CO_2$ assimilation in *Welwitschia* is a rapid phenomenon. After only 5 minutes' exposure to the source (Fig. 9), the total detectable ^{14}C activity, representing ^{14}C-labelled photosynthates, was lower in the meristematic zone than in the leaf. After 10 and 20 minutes' exposure, the activity detectable in the meristem samples was found to be considerably higher than in the corresponding leaf samples, indicating a rapid basipetal translocation of ^{14}C-photosynthates under fog conditions.

DISCUSSION

If the numerous stomata (Figs. 1—4) occurring on both leaf surfaces in *Welwitschia* are indeed the means of entry for surface water, they play a remarkable dual role, both in limiting the loss of water from the interior mesophyll, and in regulating the absorption of surface moisture when it becomes available by condensation under foggy conditions. That it is the stomata which are primarily responsible is suggested by the marked differences between uptake recorded under foggy and under föhn wind conditions. A field microscope investigation showed that, predictably, few stomata were open while the wind was blowing (Figs. 6-8). Externally-applied water appears to travel preferentially in the proximal direction towards the meristematic regions.

According to Walter (1971), the "unwettable" nature of the leaves prevents the uptake of condensed water; whereas the corky stem surface may act as a sponge. Our data indicate, however, that water applied to the leaves, without prior addition of a wetting agent, forms droplets which are readily taken up and translocated. Foliar absorption from a saturated atmosphere has been reported on another occasion in the literature (Haines, 1952).

Comparative data for CO_2 assimilation under different weather conditions are not available, since the technique of $^{14}CO_2$ application used here is appropriate only under relatively calm conditions. However, it is evident that photosynthesis proceeds at a high rate and that photosynthates are rapidly exported from the leaves in the direction of meristematic regions at the stem/leaf junction.

CONCLUSION

Since intact plants were studied under normal field conditions, the results described may safely be assumed to reflect normal physiological activities. Thus the major inference to be drawn is that atmospheric water vapour is indeed accessible to *Welwitschia* through its leaves, and hence that many of its remarkable anatomical features may be considered to have a related function. It appears that surface water may enter the leaves via the stomata which provide the only discontinuity in the relatively thick cuticle found on both adaxial and abaxial surfaces of the leaf.

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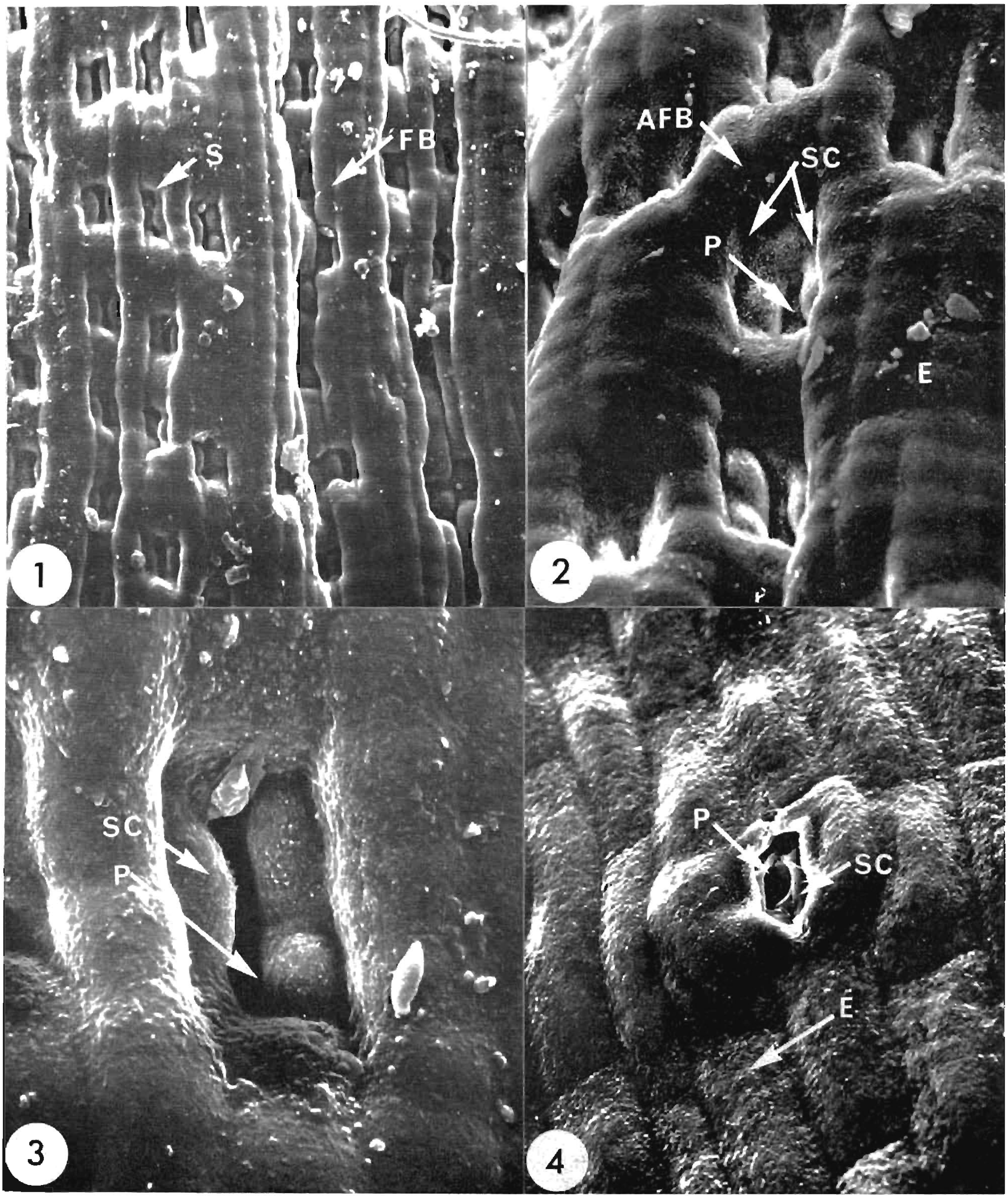
Table 1. Climatic conditions prevailing during isotope-translocation experiments.

Time	Temp. °C	RHat %	RH Wm %	Remarks
T+ 0; 9 a.m.	32,4	11	*	TPN 1,2
T+ 2; 11 a.m.	40,6	10	*	
T+ 3; 12 noon	39,4	10	*	
T+ 4; 1 p.m.	47,8	10	*	
T+ 7; 4 p.m.	34,4	19	*	
T+10; 7 p.m.	21,7	54	80	
T+23; 8 a.m.	17,8	80	94	TPN_3; $^{14}CO_2$
T+24; 9 a.m.	21,1	60	75	

RHat	Relative humidity of atmosphere.
RHWm	Relative humidity of air surrounding *Welwitschia mirabilis*.
*	Data not recorded.
TPN 1,2	Transpiration experiments Nos. 1 and 2 (Föhn-wind).
TPN 3	Transpiration experiment No. 3 (Fog).
$^{14}CO_2$	^{14}C-Photosynthesis experiments.

Table 2. Translocation of ^{14}C-photosynthates in *Welwitschia mirabilis* under fog conditions.

Exposure time (mins)	Total leaf (dpm)	Total meristem (dpm)	Mean leaf (dpm)	Mean meristem (dpm)
5,0	26 478	12 991	5 296	4 330
10,0	18 945	13 598	3 789	4 533
20,0	11 689	19 989	2 338	3 332



Figures 1—4. Scanning electron micrographs of the adaxial (Figs. 1—3) and abaxial (Fig. 4) leaf surfaces of *Welwitschia mirabilis*.
Figure 1. Low magnification showing surface features. Note stomata (S) sunken below the level of the fibre bundles (FB). x 200.
Figure 2. Higher magnification of part of upper epidermis. Cuticle, C; subsidiary cells, SC; stomatal pore, P; epidermal cell, E. Note anastomosis between some fibre bundles (AFB). x 660.
Figure 3. Detail of a stoma, upper epidermis. x 1 100.
Figure 4. Detail of a stoma, lower epidermis. x 330.

Figure 5. General layout of transpiration experiment showing liquid-scintillation vials taped to the adaxial leaf surface of an adult female *Welwitschia*. Four Pasteur pipettes are inserted in the stem adjacent to the meristematic zone.

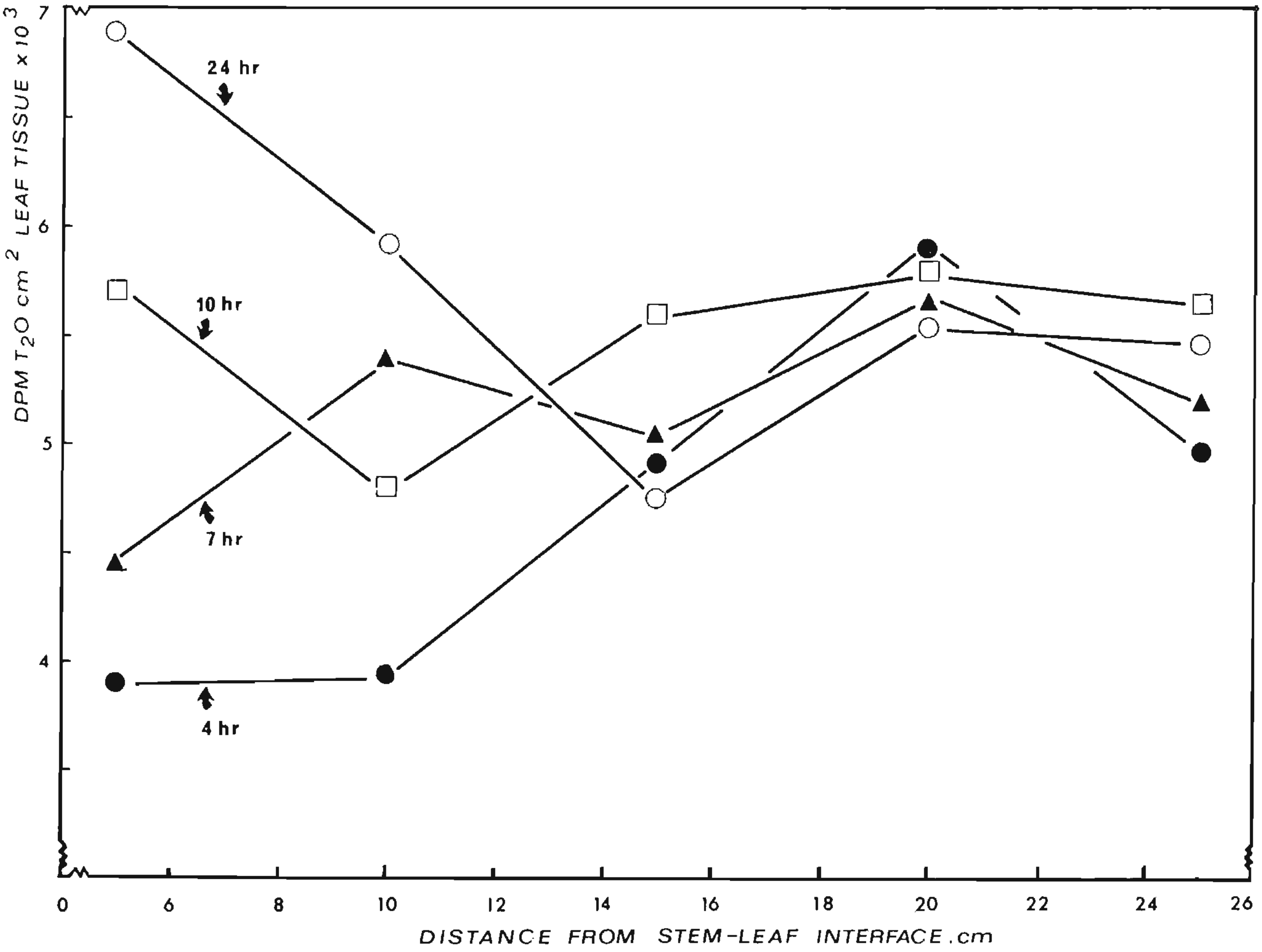


Figure 6. Results of tritiated water transpiration experiment conducted on the plant illustrated in Figure 5 under föhn wind conditions. For explanation see text.

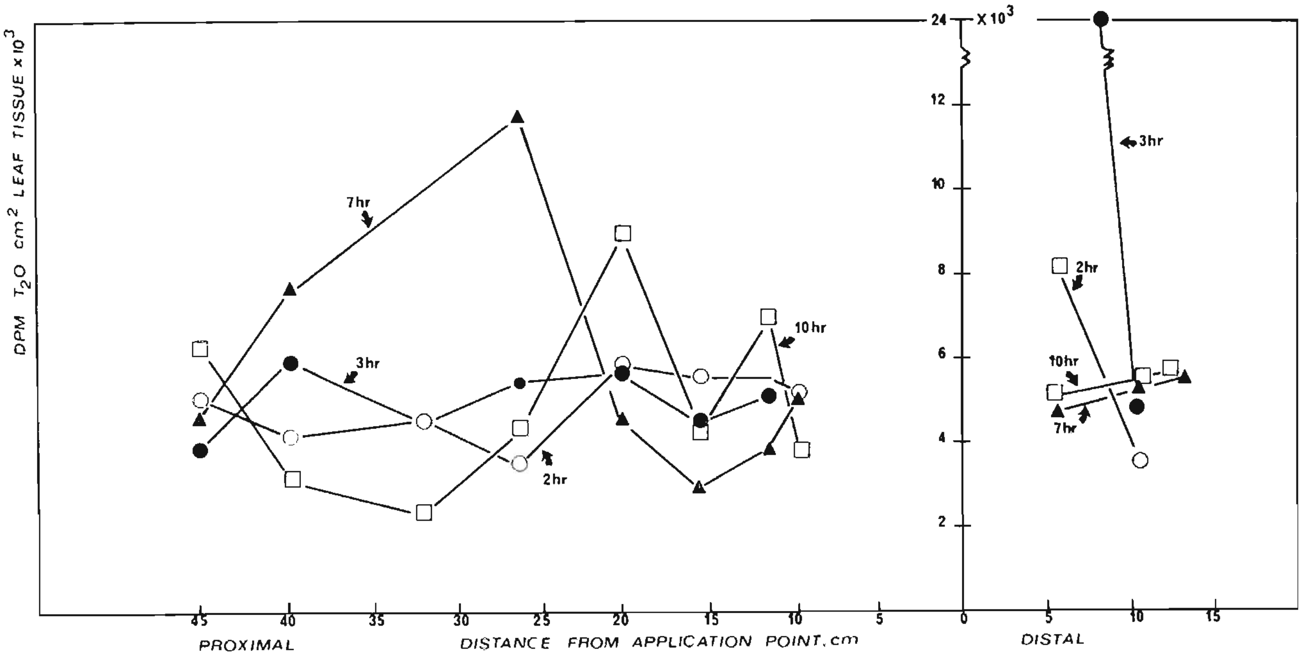


Figure 7. Translocation of radioactivity in a *Welwitschia* leaf irrigated with tritiated water, under föhn wind conditions. Note the marked fall-off of distal compared to proximal translocation.

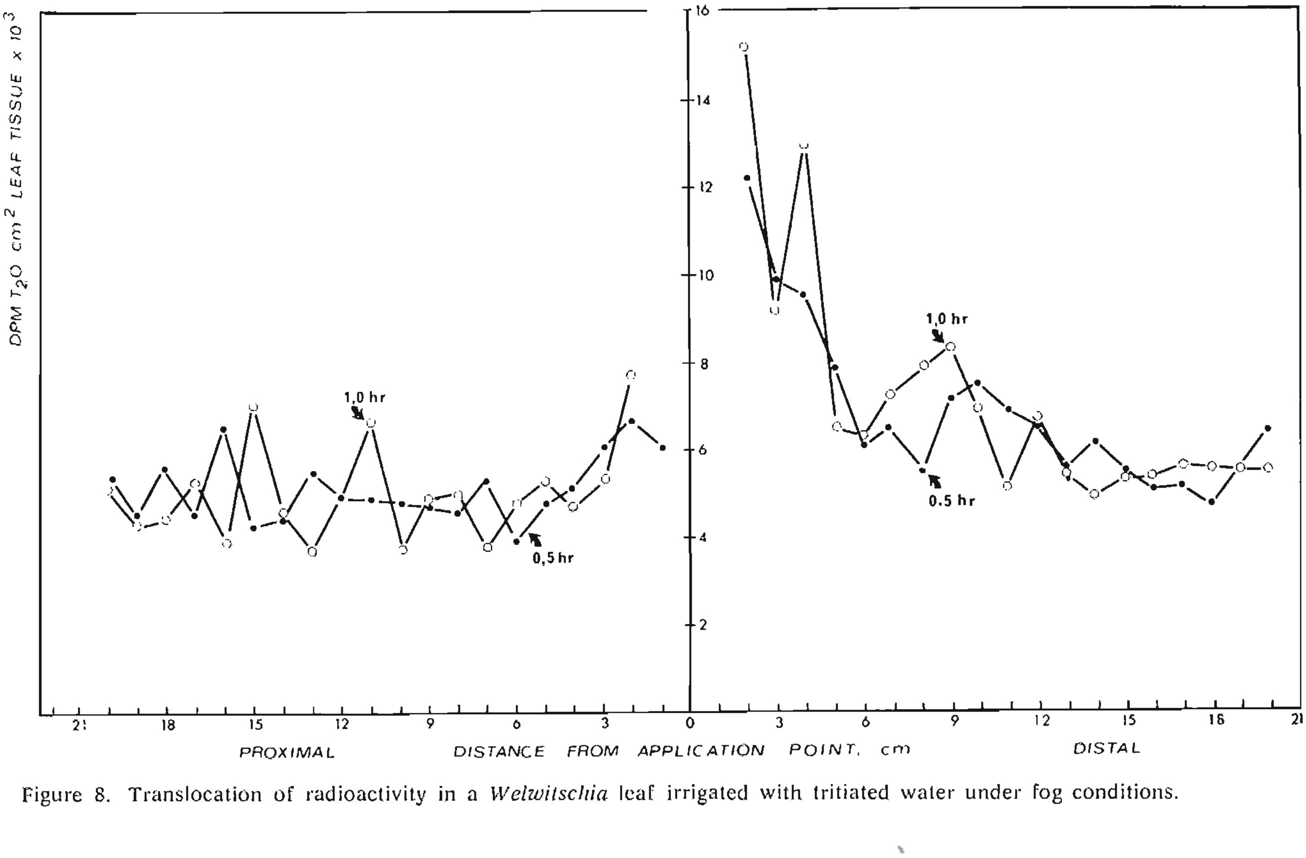
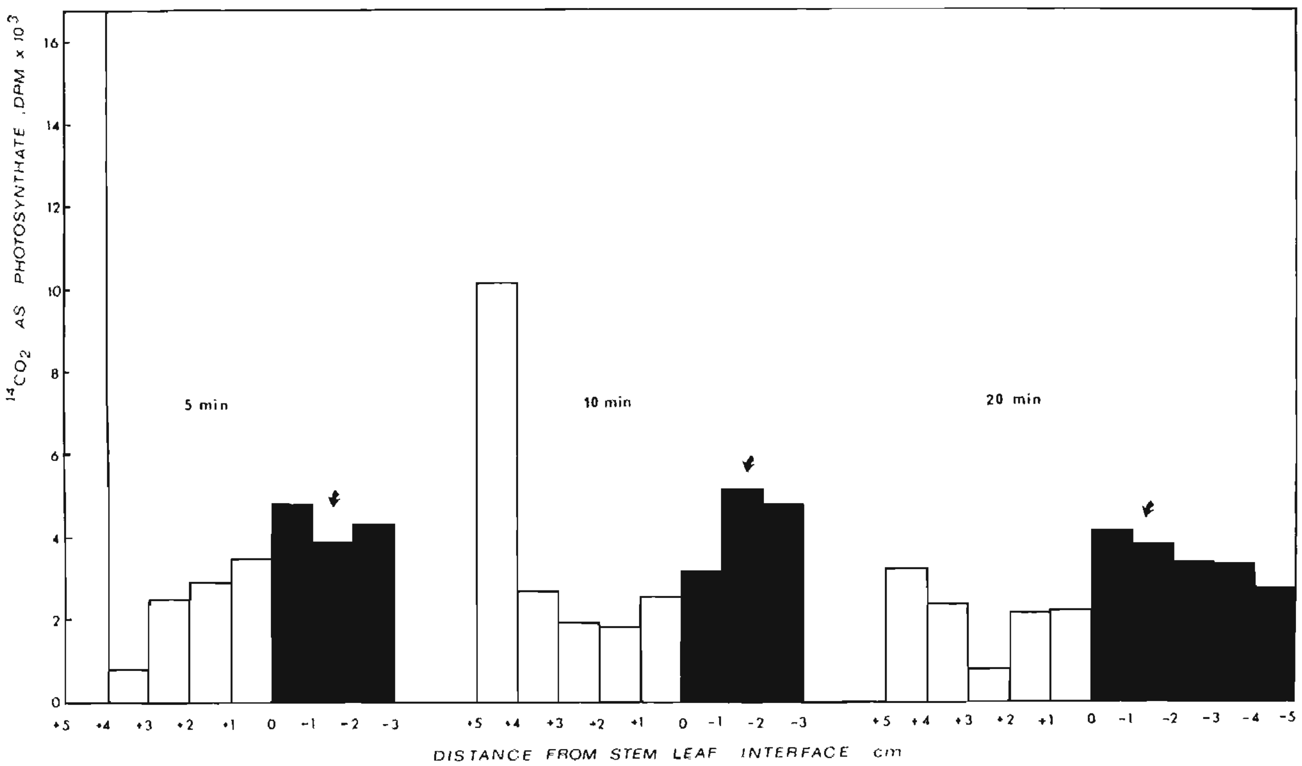


Figure 8. Translocation of radioactivity in a *Welwitschia* leaf irrigated with tritiated water under fog conditions.



Figures 9—11. Basipetal translocation of ^{14}C-photosynthates in a female *Welwitschia*. The abaxial surface was exposed for 5,0 (Fig. 9), 10,0 (Fig. 10) and 20,0 (Fig. 11) minutes. Arrows mark the approximate centres of the leaf meristem.