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STUDIES ON PHLOEM EXUDATION FROM *YUCCA FLACCIDA* HAW.

II. THE TRANSLOCATION OF ASSIMILATES

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ABSTRACT

Following the feeding of $^{14}CO_2$ to a mature leaf of *Yucca flaccida* Haw. a number of exudate fractions were collected from a bleeding inflorescence stalk.

The maximum amount of activity was collected on the third day after the application of the $^{14}CO_2$. In all the exudate fractions sucrose contained about 90 per cent of the radioactivity present.

The ^{14}C-content of the exudate exhibited a pronounced daily rhythm. The fractions which exuded during the night contained concentrations about four times those of the exudates collected during the hours of daylight. In contrast, the total dry substances and total sugar contents only showed slight daily variations. Apparently the various leaves or other parts of the plant contribute with slightly different rhythms to the solutes of the exudate.

INTRODUCTION

It has been shown that the sap bleeding from the distal part of the inflorescence stalk of *Yucca flaccida* Haw. has the properties of a phloem exudate (TAMMES and VAN DIE, 1964). A simple calculation shows that the carbohydrates present in the exudate could not have a local origin only, as the total amount secreted over a period of a few weeks exceeded the dry weight of the stalk of the inflorescence. This observation is in close agreement with the results of TAMMES (1933) obtained on *Arenga saccharifera* Labill. In this case also the sugar that exuded from the tapped inflorescence must have been translocated from elsewhere in the tree to the site of bleeding. It was also shown that carbohydrates stored in the stem of *Arenga* disappeared during bleeding.

In order to investigate the origin of the organic materials in the exudate of *Yucca flaccida* experiments were carried out on the extent of translocation of ^{14}C-labelled photosynthates from a leaf to the site of bleeding.

The experimental data are described and briefly discussed below.

METHODS

Experiments with Carbon 14. Due to its linear shape a leaf could easily be introduced into a glass tube about 70 cm long and 3 cm in diameter.

The tube was closed around the leaf basis with plasticine. The carbon dioxide was evolved at the top of the tube from a solution of ^{14}C-labelled Na_2CO_3.

All activities were measured by G. M. counting (1.6 mg/cm²) using the "infinitely thin" method. Radio-autographs were made from chromatograms by placing "Kodirex" X-ray film on the paper and developing after an exposure of 14 days.

Details of the plants used and the analytical methods have been described in a previous paper (TAMMES and VAN DIE, 1964). Kations, anions and non-ionic substances were separated with the aid of Zeo-Karb 225 and Amberlite IRA-400 in carbonate form, but at a temperature of 0–2° C.

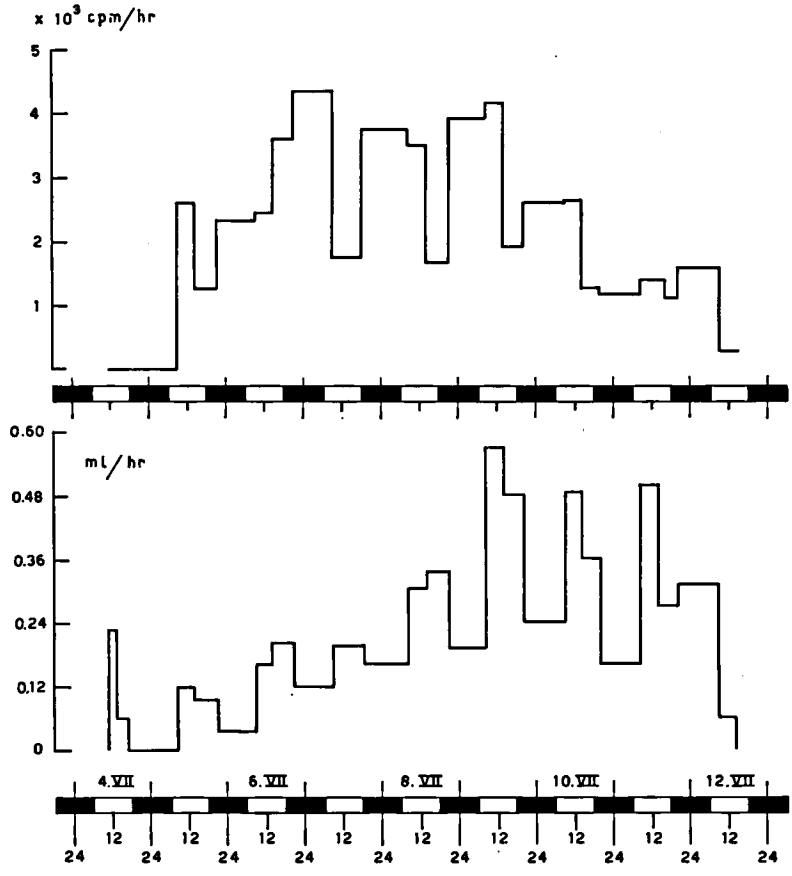

Fig. 1 (below). The relation between the rate of bleeding (ml/hr) and the periods of collection of the exudates. At the abscissa a day-night scale, subdivided at noon and midnight.

Fig. 2 (above). The relation between the rate of carbon-14 exudation (cpm/hr) and the periods of collection of the exudates.

Results

40 μ C of $^{14}CO_2$ with a total activity of 8.0×10^6 cpm was supplied to a mature leaf of a bleeding *Yucca*. It was allowed to assimilate from 10.45–11.15 a.m. Afterwards inspection with a G.M. tube showed that all detectable activity was present in the top of the leaf, near the site of the $^{14}CO_2$ generation in the assimilation tube. The leaf was about 30 cm long and the stalk about 40 cm.

The fluid exuding from the stalk was collected over a period of eight days with intervals of 3 to 15 hours. Of each fraction obtained were determined: the volume, specific activity, dry matter content, carbohydrate composition and the percentage of radioactivity present in its carbohydrate, amino acid and organic acid fraction.

The exudation rates were very low during the first few days and during the first night no exudate could be collected at all. During the following days there was a gradual increase in bleeding. As Fig. 1 shows, bleeding rates clearly demonstrated the existence of a diurnal rhythm in bleeding. The average exudation rate during the day was about twice that found at night.

Unlike the exudation rates, the specific activities of the exudate fractions showed distinct maxima at night and minima during the hours of day-light. (Fig. 3) Unfortunately the irregular bleeding during the first few hours made it impossible to obtain reliable figures for the exudation of labelled substances in this period. If the maximum values in specific activity found from the second to the eighth night are plotted logarithmically against time, a straight line results (Fig. 4). Thus there is a logarithmic decrease in ^{14}C-exudate concentration, together with diurnal variations in exudation rate and exudate concentration.

It seemed probable that both the alternating diurnal rhythms found were not wholly independent of each other. For this reason the rates of ^{14}C-exudation (= rate of exudation $\times$ specific activity) were plotted against the periods over which the labelled substances exuded. Fig. 2 again demonstrates the occurrence of a daily rhythm, but this is less pronounced than that of exudation rate or specific activity. There are no significant differences between the night and morning ^{14}C-exudation rates, but the afternoon values are considerably lower. The average ^{14}C-exudation rates for night, morning and afternoon were found to be: 2817, 2644 and 1804 cmp/hr respectively.

There was also a daily variation in sugar concentration, as also in dry matter content, but both were much less pronounced than might have been expected from the variations found in the specific activity of the exudate fractions (Fig. 6).

The distribution of radioactivity among the kations (amino acids), the anions (organic acids) and the neutral substances (sugars) were determined for several exudate fractions. The results presented in Table 1 show that the carbohydrates represented approximately 90 per cent of all activity in the exudate fractions.

Paper chromatography and subsequent autoradiography revealed

that almost exclusively labelled sucrose was present in the sugar fraction. Hardly detectable amounts of activity were found in glucose and fructose and in an unknown sugar with a low R_F-value (probably a triose).

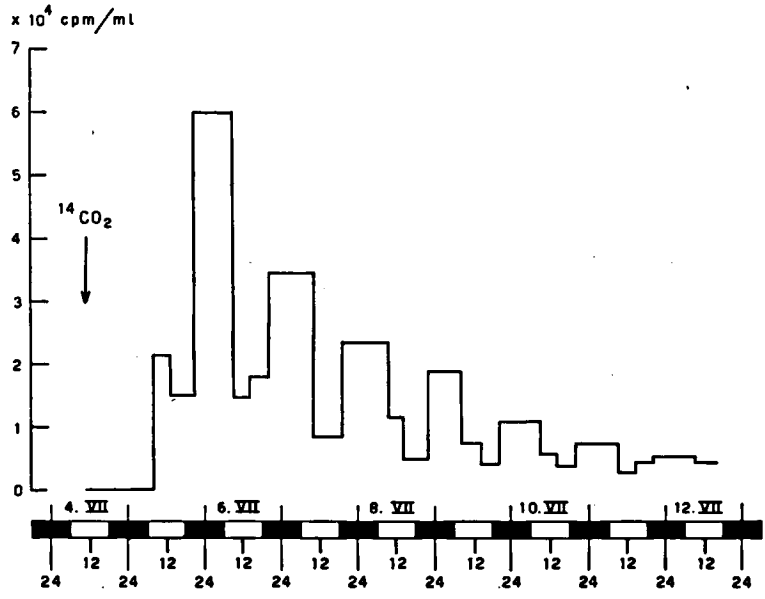

Fig. 3. The contents of carbon-14 labelled substances in the exudate fractions.

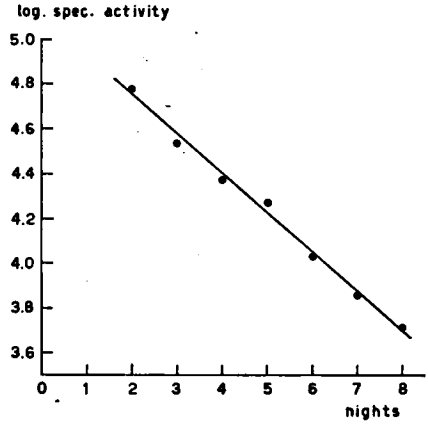

Fig. 4. The logarithmic decrease in carbon-14 content of the exudate fractions collected in successive nights.

Discussion

The daily periods of photosynthesis in the leaves of several tree species are followed by waves of relatively high sugar concentration down the bark (Mason and Maskell, 1928; Huber, Schmidt and Jahnel, 1937; Ziegler, 1956). The differences between maximum and minimum sugar concentration, reported by Huber and co-workers and Ziegler are, however, only about 3 per cent of a total concentration of about 20–25 per cent of sugar. Such relatively small differences between maximum and minimum are also found in the dry matter and sucrose contents of *Yucca* exudates. A much more pronounced rhythm, however, is found in the concentrations of

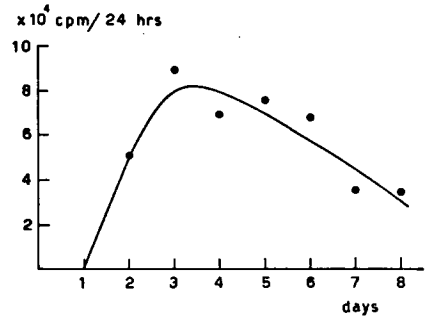

Fig. 5. The amounts of carbon-14 labelled substances exuded in successive periods of 24 hours.

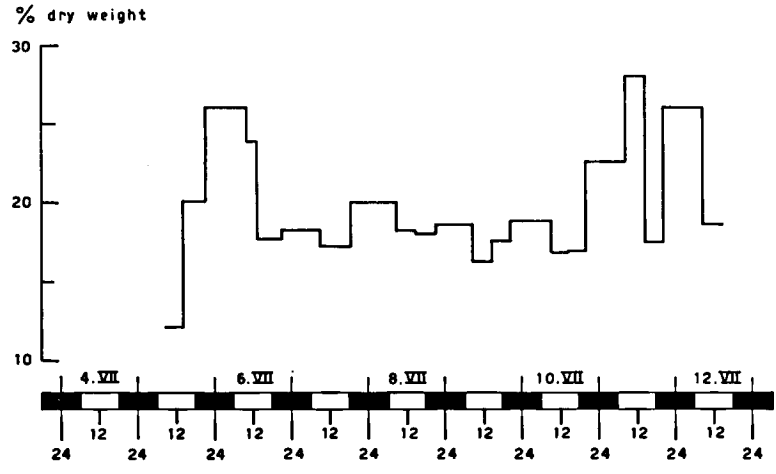

Fig. 6. The dry weights of the successive exudate fractions, expressed in weight percentages.

radioactive sucrose. This originated in one out of about 25 leaves of the plant. As it may be assumed that the other leaves or other parts of the plants have also such daily rhythms, it may be concluded that these individual daily rhythms do not all completely coincide, so

TABLE 1

The distribution of Carbon-14 among the carbohydrates, amino acids, and organic acids of some exudate fractions, expressed in percentages of total activity.

exudate fraction	carbohydrates %	amino acids %	organic acids %
8. VII	89.2	5.9	4.9
9. VII	90.4	5.6	3.9
10. VII	93.0	4.7	2.3
11. VII	89.2	8.4	2.3

that the differences between night and day concentrations in the exudate are reduced.

A remarkable observation was the relatively slow exudation of labelled substances from the stalk (Fig. 5). The greatest amount of activity exuded in the third day after the application of $^{14}CO_2$ and even on the eighth day considerable amounts of activity were secreted. Several explanations may be offered, as also for the logarithmic decrease in specific activity of the maxima of the successive nights. But without further experiments more specially directed to these phenomena, speculations on their possible explanation would be of little value.

The results obtained in the previous and present study are in close agreement with the results of TAMMES (1933, 1951). They show that the sieve tubes of several plant species can be drained for a long time, a phenomenon also described by HUBER (1953) for various *Fraxinus* species. As the exudate from *Yucca* contains only small amounts of protein, it is probably closely similar to the vacuolar fluid of the sieve tubes.

Apparently a flow of assimilates can pass the sieve tubes over a long distance and for a long time. Although it is not proved that such a flow also occurs in the intact plant, the phenomenon of the continuous phloem bleeding seems an argument in favour of the mass-movement hypothesis.

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