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作物输导系统中光合产物运输速度分析和加权平均速度测定

ANALYSIS OF PHOTOSYNTHATE TRANSLOCATION VELOCITY AND MEASUREMENT OF WEIGHTED AVERAGE VELOCITY IN TRANSPORTING PATHWAY OF CROPS

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作物输导系统中光合产物运输速度分析和加权平均速度测定

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摘　要

采用脉冲光合标记的方法，用$^{14}CO_2$标记作物成熟叶片，然后测定了标记光合产物在输导系统各点的运输图谱，通过对光合产物运输图谱从源到库沿输导系统形变的分析，证明：光合产物在作物茎鞘中不是以单一速度而是以一系列速度运输。进而建立了作物输导系统中光合产物运输加权平均速度的测定方法，试验中还以水稻和玉米作材料，实际测定了光合产物在鞘中运输的加权平均速度和最大运输速度值。

Analysis of Photosynthate Translocation Velocity and Measurement of Weighted Average Velocity in Transporting Pathway of Crops

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ABSTRACT

The translocation profile pattern of ^{14}C-photosynthate along the transporting pathway in crops were monitored by pluse-labelling a mature leaf with $^{14}CO_2$. The progressive spreading of translocation profile pattern along the sheath or stem indicates that the translocation of photosynthate along the sheath or stem proceed with a range of velocities rather than with just a single velocity. The method for measuring the weighted average velocity of photosynthate translocation along the sheath or stem was established in living crops. The weighted average velocity and the maximum velocity of photosynthate translocation along the sheath in rice and maize were measured actually.

INTRODUCTION

In the area of plant physiology, the measurement of nutrient translocation velocity in transporting pathway, for example, in sheath and stem, is difficult. By measuring the arraval rate of ^{14}C-photosynthate (^{14}C-photosynthate translocation profile) in expanding leaves on the side shoots which had developed at the older nodes along Morning Glory Vines after pluse-labelling a mature leaf with $^{14}CO_2$ and analysing the progressive spreading of the profile shape, A. Lawrence Christy and Donald B. Fisher (1977) indecated that the translocation of photosynthate in Morning Glory vines proceeded with a range of velocities rather than with just a single velocity. In most cases, we can only measure certain single velocity, for example, the maximum velocity, among the range of velocities. Obviously, this single velocity does not represent the actual velocity of photosynthate transporting along the pathway in plant.

The purpose of the present experiments was to investigate the kinetics of ^{14}C-photosynthate along sheath or stem in crops (rice and maize), to monitor the ^{14}C-photosynthate translocation profile (Kinetic curve for the changing of ^{14}C-photosynthate radioactivity with time) in monitored segements along the sheath and stem, then to analyse the progressive spreading of the profile shape along the sheath or stem. Of particular interest was to establish the method for measuring weighted averge velocity of photosynthate moving along the sheath and stem in living crops.

1 MATERIALS AND METHODS

1.1 Growth of crops

Rice (CV. Yangzhou No. 4) and maise (CV. Yi Dan No. 4) were grown in pots, which were 32 cm in height and 25 cm in inside diameter and were packed with 15 kg soil. The crops were cultured with normal managements. The experiment in 1990 was conducted with rice and maize, but in 1991 only with rice.

1.2 Labelling experiments

In 1990, when rice was 7-leaf old and maize was 5-leaf old, and in 1991, when rice was on milky stage, the second leaf from top (or the flag leaf) were sealed into a plaxiglas labelling chamber (3.5 cm diameter by 25 cm height). A light intensity of 455 $\mu Em^{-2}s^{-1}$ was supplied by one 300 W lamp, filtered through 4 cm of water. After an over-night dark period of 10 h, the light was turned on about 2 h before the labelling period. The labelling system consisted of a $^{14}CO_2$ generator, the leaf

chamber, a micro-gass pump, and interconnecting lengths of plastic tube. When labelling began, 8.88×10^7 Bq of $^{14}CO_2$ was generated from $NaH^{14}CO_3$ with 20% HCl and was pumped into the labelling chamber 15 min after generation of $^{14}CO_2$. The labelling period was terminated by removing the labelling system.

1.3 Monitoring of the ^{14}C-photosynthate translocation profile

In this experiment the mutiple-probe monitoring apparatus which connect with eight thin end-window Geiger tubes was used to monitor the ^{14}C-photosynthate translocation profile along the sheath or stem in crops. The monitoring system was shown in Fig. 1. In 7-leaf stage of rice and 5-leaf of maize, three GM tubes were fixed respectively on the labelled leaf, the top of the sheath, and the middle of the sheath, but in milky stage of rice, five GM tubes were fixed respectively on the labelled leaf, the top of the sheath, the middle of the sheath, the middle of the stem, and the ear. After labelling period terminated, the apparatus began to monitor continuously the radioactivity of ^{14}C-phetosynthate in the labelled leaf, in the monitored segements along the sheath or stem and in the ear. Then, the kinetic curve for the changing of radioactivity of ^{14}C-photosynthate in each of monitored segement along the sheath or stem with time represented the kinetic translocation profile of ^{14}C-photosynthate.

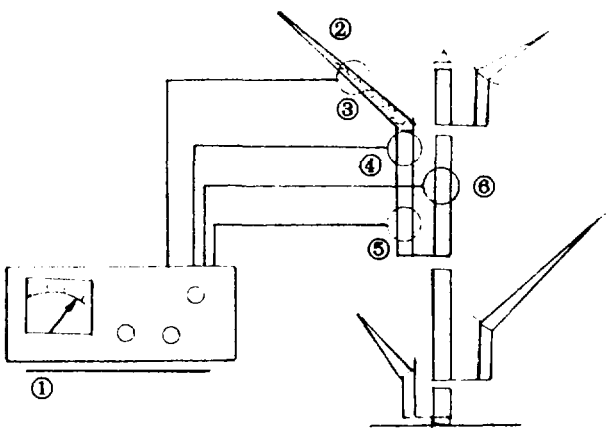

Fig. 1 The apparatus for monitoring the radioactivity of photosynthate in leaf and sheath or stem

①—— The monitoring apparatus
②—— The labelled leaf
③—— The monitored segement on labelled leaf
④—— The monitored segement 1 on the sheath
⑤—— The monitored segement 2 on the sheath
⑥—— The monitored segement on the stem

1.4 Measuring of the maximum velocity of photosynthate thanslocation

Supposed that L was the length (cm) between monitored segements on the sheath of crops, t_1 and t_2 were the time of appearance of radioactivity in segement 1 and segement 2 respectively. Hence, the maximum velocity of photosynthate translocation along the sheath could be calculated from L divided by (t_1-t_2).

1.5 Measuring of the parameters for calculating the weighted average velocity

of photosynthate translocation

L_0 is the lengths of monitored segement (cm), t_0 is the intermittent time between adjacent two monitoring (h), L_0 and t_0 could be dimensioned directly.

P is the counting efficiency of GM tube on monitored segement. If S_t was the counts rate (min^{-1}) monitored by GM tube when monitoring period terminated. After monitoring period terminated, the monitored segements were extrated in 80% boiling aqueous ethanol, and extrated aliquots was counted by a liquid scintillation spectrometer (A_{t1}, dpm). Then the extracted segement was combusted into a gaseous state, and the $^{14}CO_2$ was absorbed by scintillation cocktail. The scintillation cocktail was counted by a liquid scintillation spectrometer (A_{t2}, dpm). Thus, the counting efficiency of the GM tube could be calculated from the following expression:

$$P = \frac{S_t}{A_{t1} + A_{t2}} \times 100\% \qquad (1)$$

A is the total radioactivity of ^{14}C-photosynthate moving through the monitored segement during the total monitoring period. After monitoring period terminated, the tested plant including all roots were immediatly taken and the labelled leaves were cutted away. Then dried the tested plant in a oven, weighted a little plant sample, and combusted it into a gaseous state. The $^{14}CO_2$ was absorbed by scintillation cocktail, and counted it by a liquid scintillation spectrometer.

S_a is the adding up counts of ^{14}C-Sucrose moving through the segement monitored by GM tube in total measurement period divided by counting efficiency of the GM tube. Suposing that S'_a was the adding up counts monitored directly by the GM tube in total measurement period. Obviously, there are two fractions of ^{14}C contributing to S'_a, one is the soluble sugar (^{14}C-suerose) moving through the monitored segement, another is the insoluble substance (^{14}C-structural and stock materials) synthesised in the segment. Thus, S_a should be equal to S'_a divided by P minus the counts which the labelled insoluble substances contributed to the GM tube.

2 RESULTS AND DISCUSSION

2.1 The analysis of translocation profile and translocation velocity of ^{14}C-photosynthate along the transporting pathway in crops

The translocation profile of ^{14}C-photosynthate in the monitored segments along the sheath and stem were shown in Fig. 2 and 3. Fig. 2 shows the translocation profile along sheath and stem in rice at milky stage, and Fig. 3 shows the pro-

file along sheath in maize at 5-leaf stage. On Fig. 2, curves B, C, and D are, the translocation profile of ^{14}C-photosynthate at the top of sheath, the middle of sheath and the middle of stem respectively. Obviously, although the profile shape of B, C, D were somewhat similar, there was a progressive and fairly symmetrical spreading of the profile as they moved along the sheath or stem either in rice or in maize. Some quantitative aspects of this spreading along transporting pathway in rice were summarized in Table 1. Table 1 demonstrates the decrease in peak height, the increase in time to peak and profile width of translocation profile along the sheath or stem in crops. The increase in profile width which measured at one-half from the final point to peak on the curve proceeded at an average rate of 0. 1103 h/cm in rice. But the ratios of the time to peak to the profile width were relative constancy.

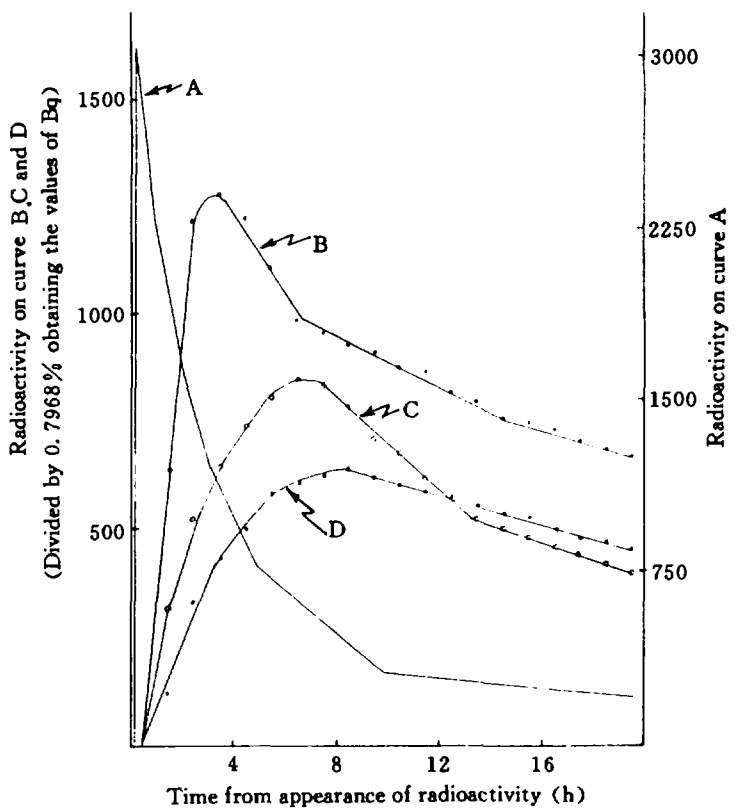

Fig. 2 The kinetic curve of radioactivity of ^{14}C-photosynthate at monitored segement along rice sheath and stem after pluse-labelling the flag leaf

A —— expected profile

B —— the profile at top of the sheath

C —— the profile at middle of the sheath

D —— the profile at middle of the stem

Since the date on the translocation profile truncated the counts which the in-

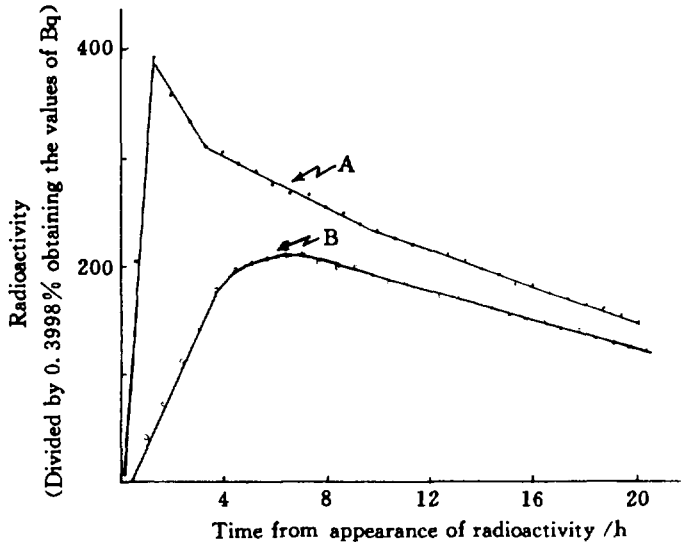

Fig. 3 The kinetic curve of radioactivity of ^{14}C-photosynthate at monitored segement along maize sheath after pluse-labelling the second leaf from top

A —— the profile at top of the sheath

B —— the profile at middle of the sheath

soluble substances (such as the starch) contributed to the GM tube. According to A. Lawrence christy et al., there were two factors being recognized as necessarily contributing to spreading in the shape of the translocation profile as it moved along the transporting pathway, exchange of sucrose between sieve elements and companion cells, and difference of structures among different sieve elements (for instance, length and area of the sieve element, the sieve plate dimensions and sieve plate pore diameters). For above two factors, the former indirectly caused some photosynthate molecules moving at lower velocities along the pathway and the latter directly caused the velocities of photosynthate's transporting stream to be different in different sieve tubes. So we think the common effect of above two factors are to cause the velocity distribution of photosynthate translocation along the pathway skewing to ward lower velocities.

Table 1 The parameters for describing the profile shape in rice at milkly stage

The segment	Parameters			
	Time to peak h	Peak hight cpm	Profile width h	Time to peak / profile width
The top of the sheath	3.0	1272	4.8	0.625
The middle of the sheath	5.0	845	7.5	0.641
The middle of the stem	7.0	641	10.8	0.648

If all of the photosynthate molecules moved with the same velocity with no less of molecules from the translocation stream, a linear displacement of the translocation profile along the pathway with the same kinetic profile would be resulted in, after a delay proportional to the distance at each segement along the pathway. This translocation profile was defined as the expected profile, as shown in curve A on Fig. 2. The data of the expected profile was calculated according to the changing of radioactivity of ^{14}C-phothsynthate remaining in source leaf (labelled leaf) as shown in Fig. 4. The expression for describing the change of radioactivity of ^{14}C-phothsynthate remaining in labelled leaf was $X = 1.5628 \times 10^5 e^{-0.3360t} + 5.4277 \times 10^5 e^{-0.00825t}$, which was taken by curve ffitting.

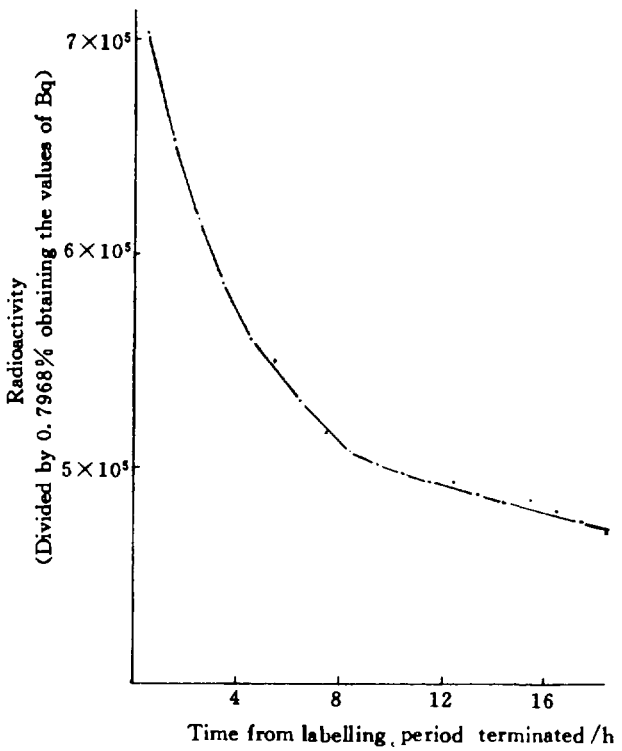

Fig. 4 The kinetic curve of radioactivity of ^{14}C-photosynthate ramaining in labelled leaf

Obviously, there was a significant difference between the expected profile (curve A) and actual one (such as curve B or C or D in Fig. 2).

According to the difference between the expected one, and the actual one and the spreading of the actual profiles shape along the pathway, it was certain that the translocation of photosynthate along sheath or stem in crops proceeded with a range of velocities rather than with just a single velocity. So it is necessary to establish a method for measuring the weighted average velocity of photosynthate translocation

along sheath or stem in living crops.

2.2 The establishment of the method for measuring the weighted average velocity and it's measuring results

In order to establish the method for measuring the weighted average velocity of ^{14}C-photosynthate translocation along the sheath in living crops, it is supposed that there are n different kinds of velocity from V_1 to V_n respectively in the sheath and stem, and there are N_i ^{14}C atoms labelled in photosynthate moving with the velocity of V_i ($i=1$ to n). If S_i means the counts which N_i ^{14}C atoms contribute radioactivity to the thin end-window GM tube fasten on the monitored segement when the N_i ^{14}C atoms (as velocity V_i) move through the segment of sheath or stem. Then the following equation could be obtained:

$$S_i = N_i \cdot \lambda \cdot \frac{L_0}{V_i} \cdot \frac{1}{t_0} \tag{2}$$

where λ is the decay constant of ^{14}C atom (min^{-1}). L_0 is the length of monitored segment (cm), t_0 is the intermittent time between adjacent two monitoring (h). From the above equation the following expression could be derived:

$$\sum_{i=1}^{n} S_i \cdot V_i = \sum_{i=1}^{n} N_i \cdot \lambda \cdot \frac{L_0}{t_0} \tag{3}$$

this leads to an equation:

$$\sum_{i=1}^{n} S_i \cdot V_i = A \cdot \frac{L_0}{t_0}$$

Where, A is the total radioactivity of ^{14}C-photosynthate moving through the monitored segment during the measurement periods. The value of A (dpm) could be counted with a liquid scintillation spectrometer by sample preparation. In addition, the counts monitored by the GM tube in total measurement periods were defined as S_a. The value of S_a (dpm) could be calculated from the value monitored directly by the GM tube divided by the counting efficiency of the tube. Thus, the expression for calculating the weighted average velocity (V_W) of photosynthate moving through the segment in crops was obtained. That is:

$$V_W \approx \sum_{i=1}^{n} \frac{S_i}{S_a} V_i = \frac{A}{S_a} \cdot \frac{L_0}{t_0} \tag{4}$$

The maximum velocity (V_m) of photosynthate moving along the sheath or and stem in living crops was listed in Table 2.

Table 2 The measured values of the maximum velocity of photosynthate moving along the sheath and stem in different crop's

Crops and growth stage			Measured item		
			Length between two segments / cm	t_2-t_1 / h	The maximum velocity / cm · h^{-1}
Rice	7-leaf stage	plant A	3.80	0.40	9.50
		plant B	4.10	0.42	9.75
	milkly stage		91.30	2.917	31.299
Maize (5-leaf stage)			2.57	0.38	6.75

t_1 is the time for ^{14}C-photosynthate appearance at segment 1.

t_2 is the time for ^{14}C-photosynthate appearance at segment 2.

Table 2 indicates that there is a significant variance between the V_m at 7-leaf stage and at milky stage in rice, the V_m at milky stage is much heigher than that at 7-leaf stage. This variance appeared to be caused partly by an acceleration of the growth of ear.

Table 3 illustrats the values of the weighted average velocity (V_W) of photosynthate moving along the sheath in living crops and the deta of parameter for calculating V_W.

Table 3 The measured values of V_W and parameters for calculating V_W

Crops and growth stage			Measured item						
			t_0 / h	L_0 / cm	A / $\times 10^6$ dpm	S'_a / cpm	P / %	S_a / $\times 10^7$ dpm	V_W / cm · h^{-1}
Rice	7-leaf stage	plant A	0.1333	1.800	4.896	70991	0.6610	1.074	6.156
		plant B	0.1333	1.800	5.245	72280	0.6500	1.112	6.370
	milkly stage		0.2000	1.800	29.050	89779	0.7968	1.1267	23.205
Maize (5-leaf stage)			0.1333	1.800	2.203	23549	0.3998	5.887	5.503

It is obvious that the maximum velocity and the weighted average velocity are different. In any case, the weighted average velocity is lower than the maximum velocity of photosynthate translocation along the sheath in crops.

The all ratios of the weighted average velocity to the maximum velocity ($V_W/V_m = 0.7414$ in rice at 7-leaf stage, $= 0.691$ in rice at milky stage, $= 0.749$ in maize at 5-leaf stage) are larger than 0.5. This indicates that although the distribution of photosynthate translocation velocity skews toward lower velocities, it is apparent that most of photosynthate molecules move at relatively higher velocity along the sheath in living crops.

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