1973

The Effects of Exposure to Darkness on Sugar Translocation in Straight-Neck Squash

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THE EFFECTS OF EXPOSURE TO DARKNESS ON SUGAR TRANSLOCATION IN STRAIGHT-NECK SQUASH

(TITLE)

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THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1973
YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING
THIS PART OF THE GRADUATE DEGREE CITED ABOVE

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AKNOWLEDGEMENTS

The author is sincerely indebted to Dr. T. M. Weidner whose persistent patience and guidance made the initiation and completion of this investigation possible. A debt of thanks is also due to Dr. W. Scott, Dr. R. Darding, and Dr. R. Smith for their helpful suggestions in the completion of this manuscript.

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THE EFFECTS OF EXPOSURE TO DARKNESS ON SUGAR TRANSLOCATION IN STRAIGHT-NECK SQUASH

It is common knowledge to investigators of sugar translocation that the living sieve tube elements are the channel by which carbohydrates manufactured in the leaves are dispersed throughout the body of the plant (3,13,14,19). The question of how translocated substances move throughout the plant elicits considerable controversy and continues to stimulate investigation.

There are three main theories which have been proposed to explain the mechanism of organic translocation. The theory of mass flow, as proposed by Münch (3,14) in 1927, explains the movement of translocated substances as an effect caused by varying concentration gradients between the source, which is usually the leaf, and the sink, which is an area in the plant of lower sugar concentration. Although this theory is widely accepted, it does not explain bidirectional translocation within the same sieve tube element (1,20).

Fensom (5) and Spanner (15) proposed the electrokinetic theory. Their theory is based on a potassium-ion pump mechanism which is responsible for the movement of solutes along

the sieve tubes and through the sieve plates. This theory has received relatively little support.

A third theory, presented by Thaine and supported by others (1,16,17,18,20), introduces the concept of translocation along or through protoplasmic strands. In his theory of protoplasmic streaming, Thaine (17) presents evidence that protoplasmic strands have been seen in sieve tube elements and that small particles the size of mitochondria (about 0.5 u in diameter) have been photographed traveling along these strands. Thaine concludes that there is evidence of biderectional translocation in the same sieve element. Experimental evidence has shown that while on one strand the particles are moving in one direction, on another strand within the same sieve element the particles can be seen traveling in opposite direction. Trip and Gorham (20) and Biddulph and Cory (1) have also presented evidence supporting bidirectional translocation. Esau (4) does not support this theory; she holds that the transcellular strands are mere artifacts caused by diffraction.

The study reported here is concerned with straightneck squash because considerable experimental work concerning translocation has been done with this plant. Numerous studies (10,12,21,22,23,24,25) have shown that stachyose,

sucrose and raffinose are the main transport molecules in this species. Webb (21) using C^{14} in his experiment with squash presented experimental data which showed that 50% of all assimilated C^{14} was incorporated into the plant as stachyose and sucrose.

Some work has been done concerning the effect on the rate of translocation when a plant is exposed to darkness. Work with sugar beet (Beta vulgaris L. cultivar) by Geiger et al. (6) using C^{14} has shown that translocation from a source leaf when exposed to darkness has a reduced translocation rate of 50% of normal at 60 minutes into the dark period and a translocation rate of 25% at 150 minutes into the dark period as compared to the rate of translocation in full lighting conditions. Experiments by Hartt et al. (7,-8,9), using sugar cane, provided evidence showing that leaves subjected to dark periods had a decrease in the rate of translocation. They supported their evidence by concluding that the apparent decrease in translocation is not necessarily due to a decrease in the rate of translocation but rather to a photosynthetic shut down during the dark period. Hartt (9), using C^{14}, has shown that the sugars translocated during the day are those that have incorporated radioactive carbon and that sugars that are translocated by night are

those that were made by conversion from other labeled compounds such as organic acids, organic phosphates, and various insoluble residues.

This study will examine the effect that darkness may have on the quantity and quality of sugars translocated in straight-neck squash.

Materials and Methods

Young straight-neck squash plants (*Curcurbita pepo L.* variety *melopepo torticollis*) were used during this investigation. Because of a bacterial disease (angular leaf spot, causal agent *Pseudomonas lacrymans*) which repeatedly infected young seedlings, it was necessary to perform the following sterile technique. Seeds were first soaked for 45 seconds in a 5% Clorox solution (5 ml of Clorox in 95 ml distilled water). This solution was drained off and the seeds were then immersed in a 50 mg/500 ml solution of $HgCl_2$ in water for an additional period of 45 seconds. The seeds were then placed on moist Whatman #1 filter paper in a sterilized Petri Dish for a period of 4 days. At the end of this time period, the germinating seeds were transferred to a bell-jar apparatus in which the seedlings were placed on cheesecloth over an aerated 10^{-4} M $CaSO_4$ solution for an additional 4 days (All materials used in the bell-jar apparatus were autoclaved to ensure sterility).

At the end of the second 4-day period the seedlings were transferred to a Sherer Controlled Environment Chamber. Prior to this transfer the following precautions were taken to decrease the contamination present in the chamber. The chamber was first washed with a 10% Clorox solution.

A spray of 5 grams/liter of Captan 50-WP was used to control those organisms that were suspected as being the infective agent hindering the growth of the squash seedlings (Captan 50-WP is specific for controling angular leaf spot). The ingredients of Captan 50-WP are presented on Table 1.

Table 1

Ingredient	Percent Weight
Captan N{(trichloromethyl) thio)-4 cyclohexene-1,2 dicarboximede	50%
Inert Ingredients	50%

After the Captan 50-WP had been sprayed, the chamber was sealed for a period of 24 hours. The seedlings were transferred into the prepared chamber and placed on an aerated mineral solution. The composition of the modified Hoagland mineral solution used is given in Table 2. All materials used in the growing of the squash in the chamber were either autoclaved or washed in a 5% Clorox solution to ensure sterility. After a period of 4 days in the growth chamber, the seedlings were sprayed with a fine spray of Captan 50-WP at the same concentration previously mentioned. This spraying technique was repeated each week thereafter for a period of three weeks.

During their time in the growth chamber, the squash plants were exposed to a 16-hour light period and an 8-hour

Table 2. Modified Hoagland Mineral Solution

$Ca(NO_3)_2$	3×10^{-3} M
KH_2PO_4	2×10^{-3} M
KNO_3	2×10^{-3} M
$MgSO_4$	2×10^{-3} M
H_3BO_3	800×10^{-7} M
$MnCl_2$	150×10^{-7} M
$ZnCl_2$	15×10^{-7} M
$CuCl_2$	8×10^{-7} M
MoO_3	7×10^{-7} M
Fe (as Fe-EDTA)	900×10^{-7} M

dark period. The light intensity was about 1,000 foot candles at the level of the plants. The light period temperature was 24° C and that of the dark period was 19° C. The light was furnished by four 150 watt cool-white fluorescent tubes and eight 25-40 watt incandescent light bulbs.

At the end of 21 days in the growth chamber the plants were removed for experimentation. The petiole from node 5 was used throughout this study.

Experimental Procedures

The experiment began with the termination of a 16-hour light period. At each interval of 0,30,90, and 150 minutes into dark period, the petioles from node 5 were removed from three different plants and placed in dark conditions in the lab. Each petiole was then cut into 6 or 7 2-cm sections which were weighed individually on a Sartorius analytical balance to the nearest 10^{-2} gram. The individual sections were then placed into test tubes containing 10ml of hot 80% ethanol in water. This was followed by storage at -25° C. Later, each section was extracted in a soxhlet extractor with hot 80% ethanol in water for a period of three hours. At the end of this time period the samples were diluted to 25 ml with 80%

ethanol and stored at -25° C until the determination of total and individual sugars could be performed.

Tests for the Determination of Total and Individual Sugars

Preparations of the samples for total and individual sugar determinations were modified from the techniques previously used by Nicholson (12) and Youngdahl (25). Quantitative tests with known amounts of stachyose, raffinose, and sucrose at the concentrations used by Nicholson and Youngdahl may have yielded erroneous data. A discussion of modifications used to correct this potential error will be discussed below.

It was concluded from quantitative tests for the determination of total sugar concentration that it would be necessary to use 5 ml of the total 25 ml sample to obtain valid results colorimetrically. Nicholson, in his total sugar determinations, used only 1 ml of his total sample volume of 100 ml. It was found necessary to use 20 times the amount that Nicholson used to obtain repeatable results.

Total sugar determinations of the sugars in each sample were achieved by the following technique. Five ml of each sample was placed into a test tube and evaporated until dry with the use of a Rotary Evapo-Mix under reduced pressure with a water bath temperature of 65° C. Then, one

ml of distilled water was added to each test tube. The water was then mixed vigorously in the test tube to dissolve all of the sugars. Following this, three ml of anthrone reagent (100 mg of anthrone dissolved in 50 ml of concentrated sulfuric acid) was added to each test tube. The anthrone reagent and water was then mixed thoroughly with a Vortex Junior mixer. This mixture was then heated for 10 minutes in a water bath at 100° C. The samples were then cooled in an ice bath and the contents of each sample were transferred to colorimetric tubes, which were then tested at 620 nanometers in a Bausch and Lomb Spectronic 20 compared with an anthrone-water blank. Tests conducted in this laboratory have shown that each 0.01 optical density unit represents approximately 1 µg of sugar.

For the determination of individual sugar concentration in each sample, 5 ml of the sample was transferred to a test tube and then evaporated to dryness by the method previously described. In their studies Nicholson and Youngdahl used only 1% of their sample volume as compared to the 20% of the sample used in this study. Approximately 1 ml of distilled water was added to the sample and the sugars present in the test tube were dissolved into solution with the use of a Vortex Junior mixer. The entire sample

was then spotted on Whatman #1 chromatograph paper with the use of a micropipettor. Approximately 50 ul of a 1% sucrose, 1% stachyose, and a 1% raffinose solution were spotted on the side strip. The samples were allowed to dry on the paper before being placed into the chromatograph jar. The chromatograms were developed in a descending flow of 1-butanol: acetic acid: and water (3:3:2:) solvent for a period of 24 hours. At the end to this time period, the chromatograms were dried in a forced draft chromatography oven for 10 minutes at 100° C.

The side strips, each 1 3/4 inches in width, were cut from the chromatograms. The known sugars stachyose, raffinose, and sucrose, were located on the side strips with a benzidine spray reagent. The benzidine spray reagent consisted of 0.5 mg of benzidine in 10 ml of 40% of (w/v) trichloroacetic acid in water, 10 ml of glacial acetic acid, and 80 ml of 95% ethanol in water. After spraying, the side strips were developed in the forced draft chromatography oven at 100° C for 10 minutes. The portions of the chromatograms containing these three sugars were cut out (each strip was cut exactly one inch wide in width) and the sugars were eluted into test tubes with approximately 1 ml of water in an elution chamber. The eluted sugar was then

dried with the Rotary Evapo-Mix as before. The amount of sugar present in each sample was then determined with the use of the anthrone and the Sprectronic 20 by means of the procedures previously outlined. Tests conducted indicated that for each 0.1 optical density unit there was 0.7 µg of sucrose, 0.8 µg of raffinose, and 1.2 µg of stachyose.

A Discussion Concerning the Variations in the Amount of Sample Used For the Determination of Total and Individual Sugars.

It was concluded from preliminary tests that there are inherent errors in the procedures used for the determination ot total and individual sugars. It was determined that the sample size used by Nicholson (12) and Youngdahl (25) may have led to data containing percentage errors so large as to render their conclusions invalid. It was found that an increased sample size made it possible to reduce the percentage of error and to obtain valid and reproducible data. It is assuned that this change in sample concentration used has enhanced the accuracy of the data collected during this study.

Results

The values for the total sugar determination are presented in Tables 3 and 4. Figures 1 and 2 graphically illustrate the variations in total sugar concentraions at 0, 30, 90 and 150 minutes after the beginning of the dark period. Figure 1 illustrates the gradual decrease in sugar concentration of each petiole as the dark period continues. The gradual upswing of each line on the graph may be explained by a decrease in petiole section weight rather than by an increase in total sugar concentration. It is assumed that there is a fixed amount of sugar traveling through the petiole at any given moment and that it is equally distributed. So although, there appears to be an increase in total sugar concentration in the petiole sections nearest the leaf blade it is likely due to the decrease in petiole section weight per cm from base to leaf blade. This observation has also been reported by Webb and Gorham (23).

Figure 2 illustrates the fluctuations in total sugar of the individual sections over the four experimental time periods. As the periods of time during the darkness increase, there is also a decrease in total sugar concentration per petiole section.

The values for the individual sugar determinations

are presented on Tables 3 and 4. Figures 3,4,5, and 6 illustrate the variations in stachyose and sucrose concentration over the four periods of time during darkness. Raffinose, although listed in the tables, is not graphed since it is not considered a major transport molecule. Figure 3 illustrates that at 0 time in the dark, the concentration of sucrose is higher than that of stachyose. This result was expected, since studies with young leaves (21) have shown that sucrose is the main transport molecule and that it is not until the leaf is mature that the main transport molecule becomes stachyose. Figure 4, at 30 minutes into the dark period, shows that stachyose and sucrose concentrations have both decreased substantially. Sucrose still appears to be present in a higher concentration than stachyose. Figure 5, at 90 minutes into the dark period, demonstrates stachyose and sucrose continuing to level off. The amoutns of sugar present in the petiole have decreased and are becoming stable. Figure 6, at 150 minutes into the dark period, shoes a continuing of this leveling off of stachyose and sucrose. This leveling off can be attributed to the fact that since the lights in the chamber had shut down, so did photosynthesis and the production of new sugar. Work done by Hartt and Korshak (9) supports this conclusion; further, they conclude that sugars translocated during the

Table 3.

Comparison of total sugars and individual sugars at 0 and 30 minutes into the dark period in 2-cm sections of petiole from node 5.

0 Minutes into Dark Period

2 cm section	weight (g)	total sugars (mg)	stachyose (mg)	sucrose (mg)	raffinose (mg)
1	0.25	1.13	0.14	0.37	0.19
2	0.19	1.26	0.24	0.33	0.21
3	0.14	1.38	0.55	0.36	0.79
4	0.12	1.43	0.33	0.80	0.19
5	0.10	1.71	0.59	0.92	0.32
6	0.09	1.84	0.55	0.62	0.28
7	0.09	2.33	----	----	----

30 Minutes into Dark Period

2 cm section	weight (g)	total sugars (mg)	stachyose (mg)	sucrose (mg)	raffinose (mg)
1	0.29	0.89	0.16	0.20	0.12
2	0.21	1.04	0.16	0.28	0.16
3	0.18	1.14	0.28	0.23	0.35
4	0.14	1.33	0.19	0.34	0.09
5	0.12	1.35	0.23	0.27	0.31
6	0.10	1.68	0.17	0.04	0.34
7	0.08	1.86	----	----	----

Table 4.

Comparison of total sugars and individual sugars at 90 and 150 minutes into the dark period in 2-cm sections of petiole from node 5.

90 Minutes into Dark Period

2 cm section	weight (g)	total sugar (mg)	stachyose (mg)	sucrose (mg)	raffinose (mg)
1	0.28	0.96	0.15	0.19	0.15
2	0.20	0.96	0.20	0.18	0.20
3	0.17	1.02	0.24	0.27	0.18
4	0.13	1.11	0.22	0.30	0.19
5	0.12	1.22	0.28	0.37	0.23
6	0.09	1.35	0.33	0.33	0.33
7	----	----	----	----	----

150 Minutes into Dark Period

2 cm section	weight (mg)	total sugar (mg)	stachyose (mg)	sucrose (mg)	raffinose (mg)
1	0.32	0.84	0.09	0.11	0.06
2	0.26	0.82	0.19	0.13	0.28
3	0.20	0.93	0.18	0.16	0.18
4	0.17	1.02	0.21	0.21	0.11
5	0.15	1.09	0.27	0.24	0.21
6	0.12	1.34	0.29	0.18	0.15
7	0.10	1.54	----	----	----

Fig 1. Total sugar in 2-cm sections of petiole over four periods of time after the begining of the dark period.

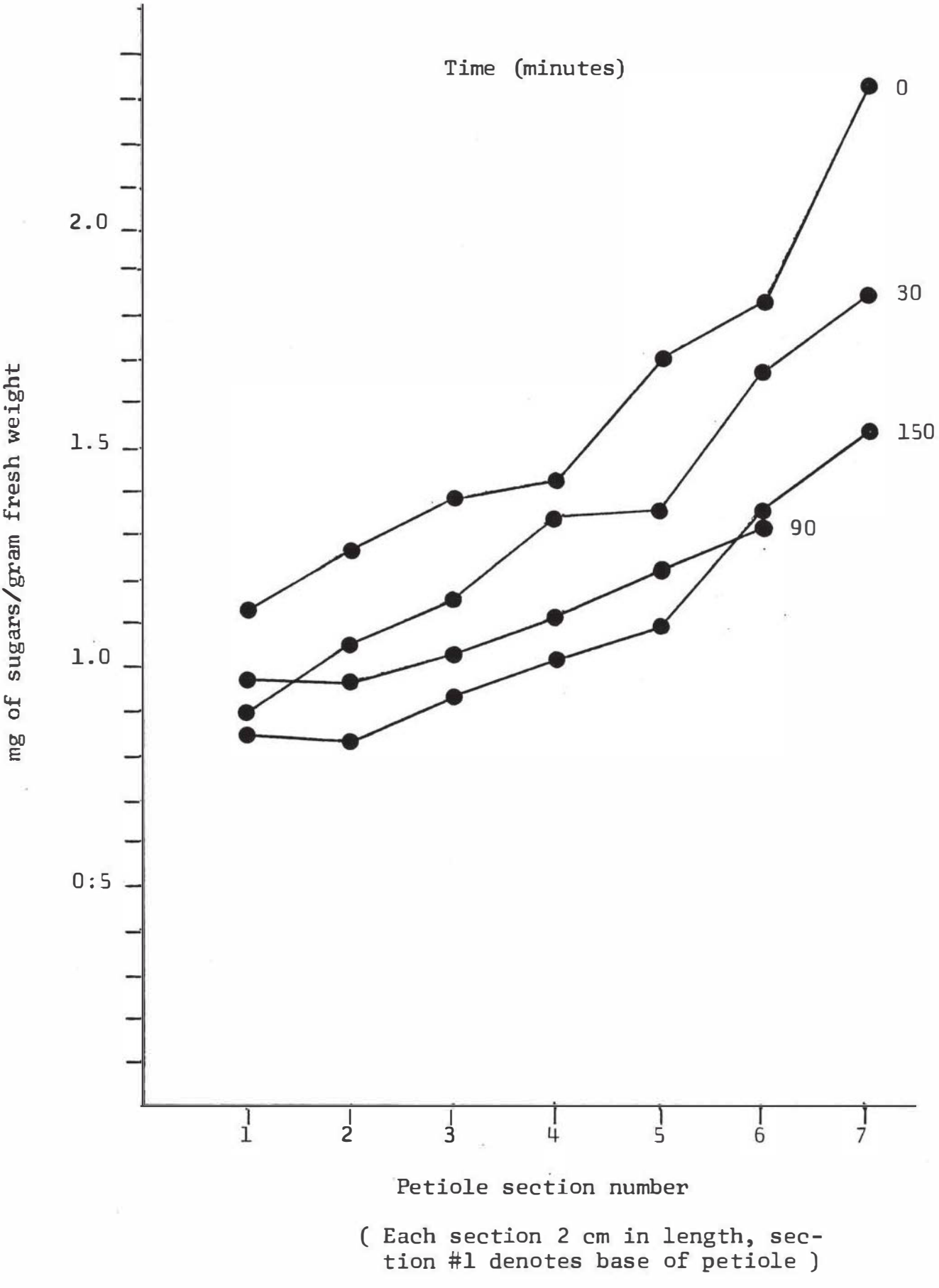

Time (minutes)
0
30
90
150
2.0
1.5
1.0
0:5
mg of sugars/gram fresh weight
1
2
3
4
5
6
7
Petiole section number
(Each section 2 cm in length, section #1 denotes base of petiole)

Fig. 2 Changes in total sugar of individual petiole sections over the four periods of time after the begining of the dark period.

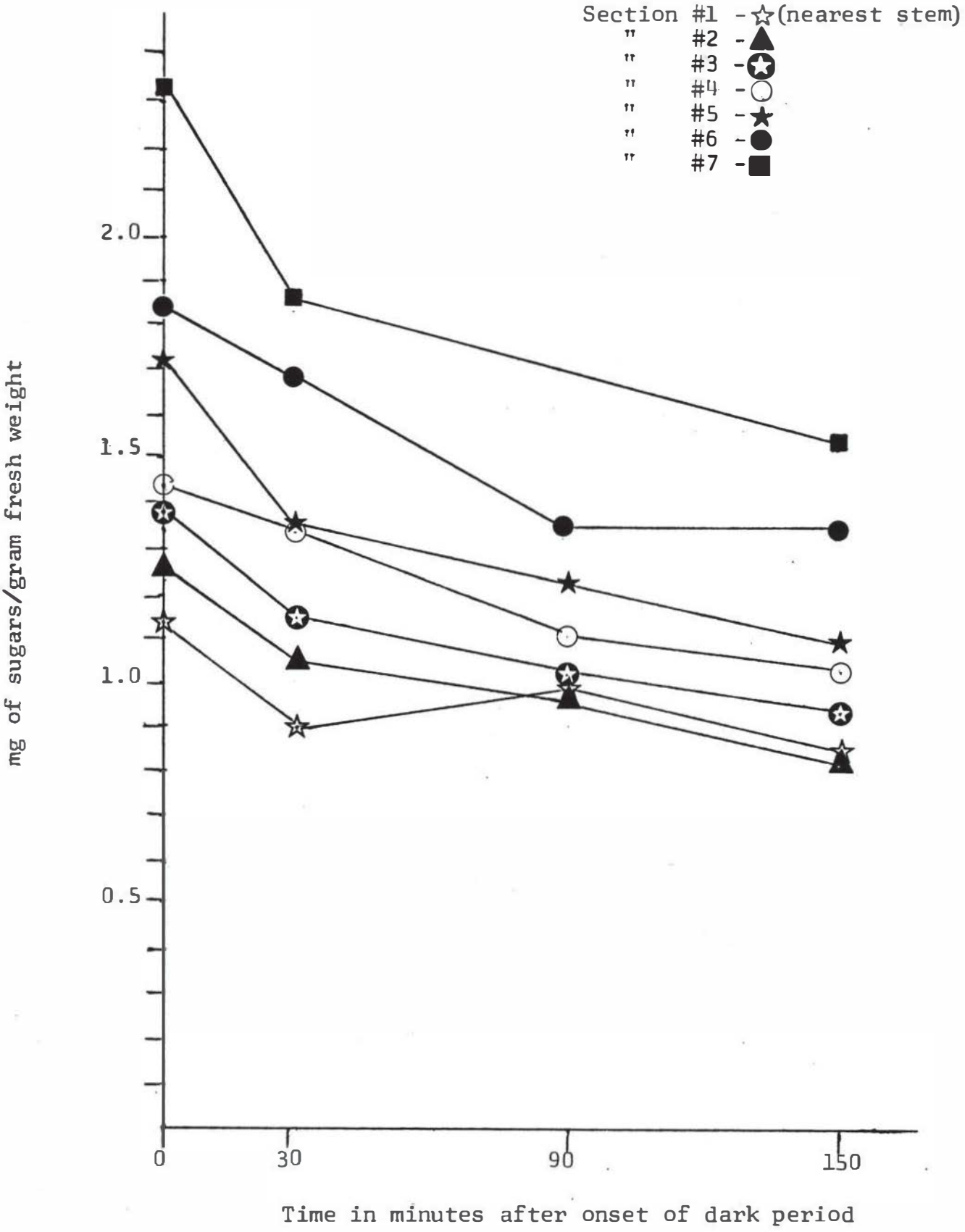

Section #1 - ☆(nearest stem)
" #2 - ▲
" #3 - ✪
" #4 - ○
" #5 - ★
" #6 - ●
" #7 - ■
2.0
1.5
1.0
0.5
mg of sugars/gram fresh weight
0
30
90
150
Time in minutes after onset of dark period

Fig. 3 Concentrations of stachyose and sucrose in 2-cm petiole sections at 0 time after the begining of the dark period.

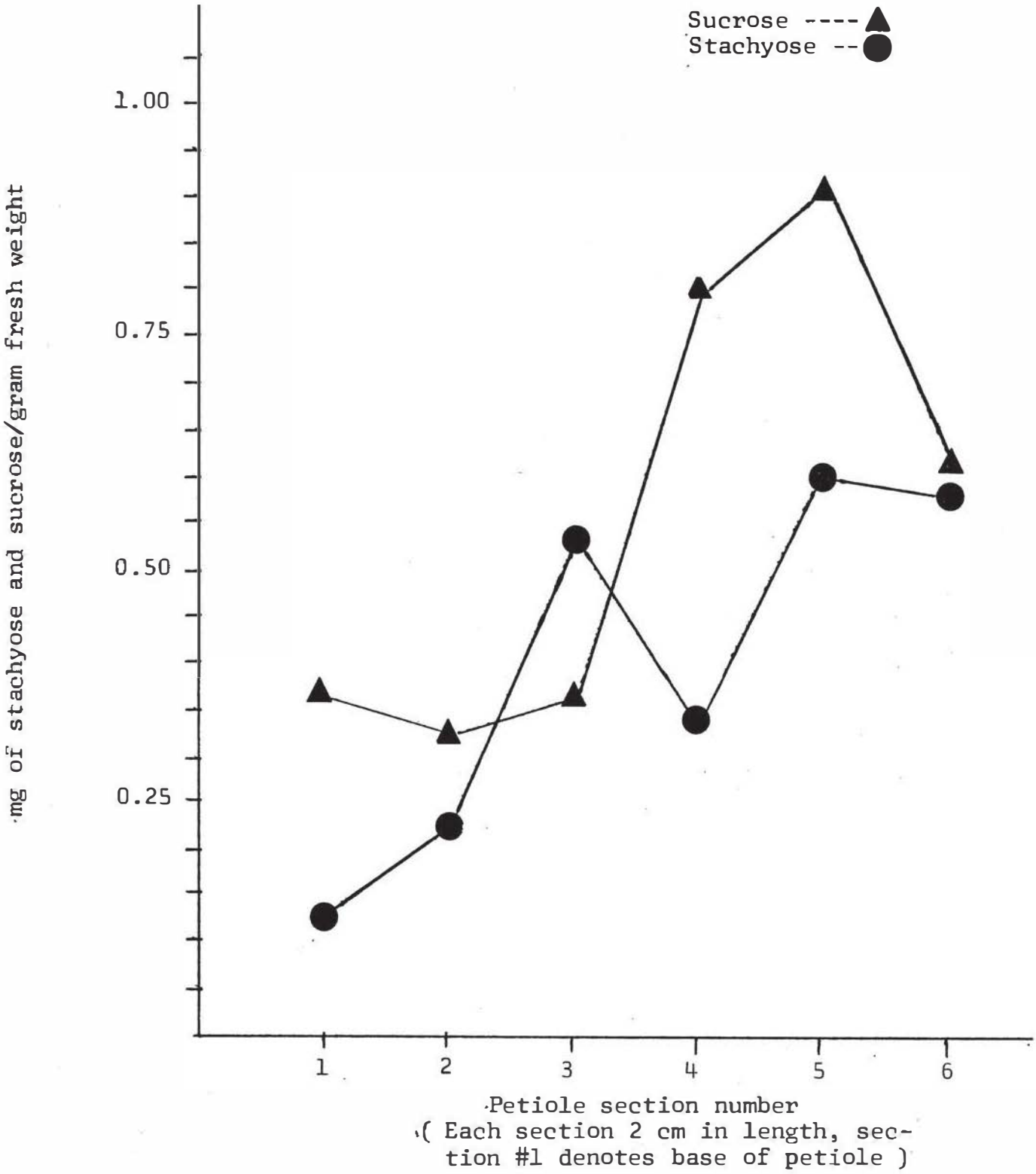

Sucrose ----
Stachyose --
1.00
0.75
0.50
0.25
mg of stachyose and sucrose/gram fresh weight
1
2
3
4
5
6
Petiole section number
(Each section 2 cm in length, section #1 denotes base of petiole)

Fig. 4 Concentrations of stachyose and sucrose in 2-cm petiole sections at 30 minutes after the begining of the dark period.

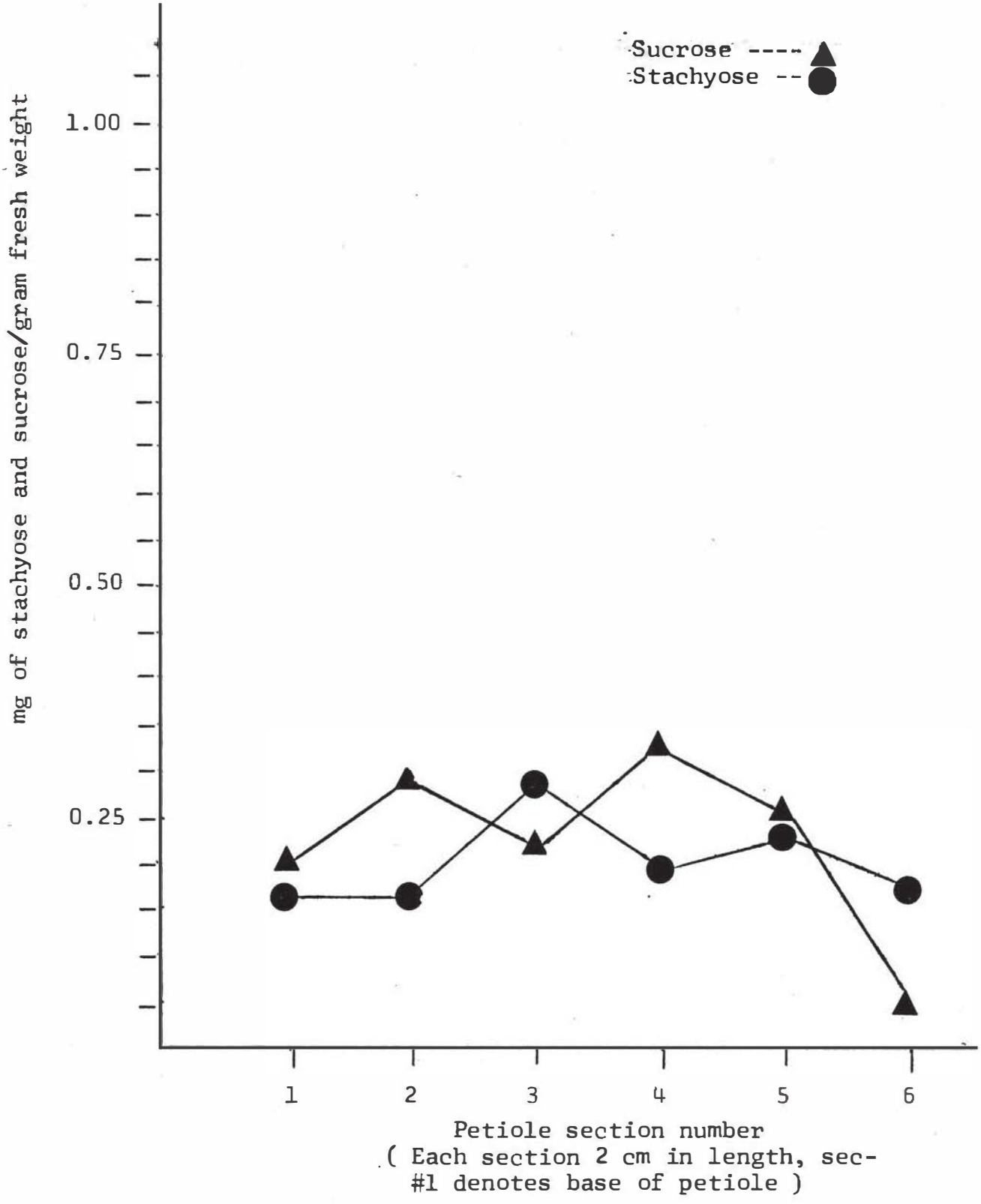

Sucrose ----
Stachyose --
mg of stachyose and sucrose/gram fresh weight
1.00
0.75
0.50
0.25
1
2
3
4
5
6
Petiole section number
(Each section 2 cm in length, sec-
#1 denotes base of petiole)

Fig. 5 Concentrations of stachyose and sucrose in 2-cm petiole sections at 90 minutes after the begining of the dark period.

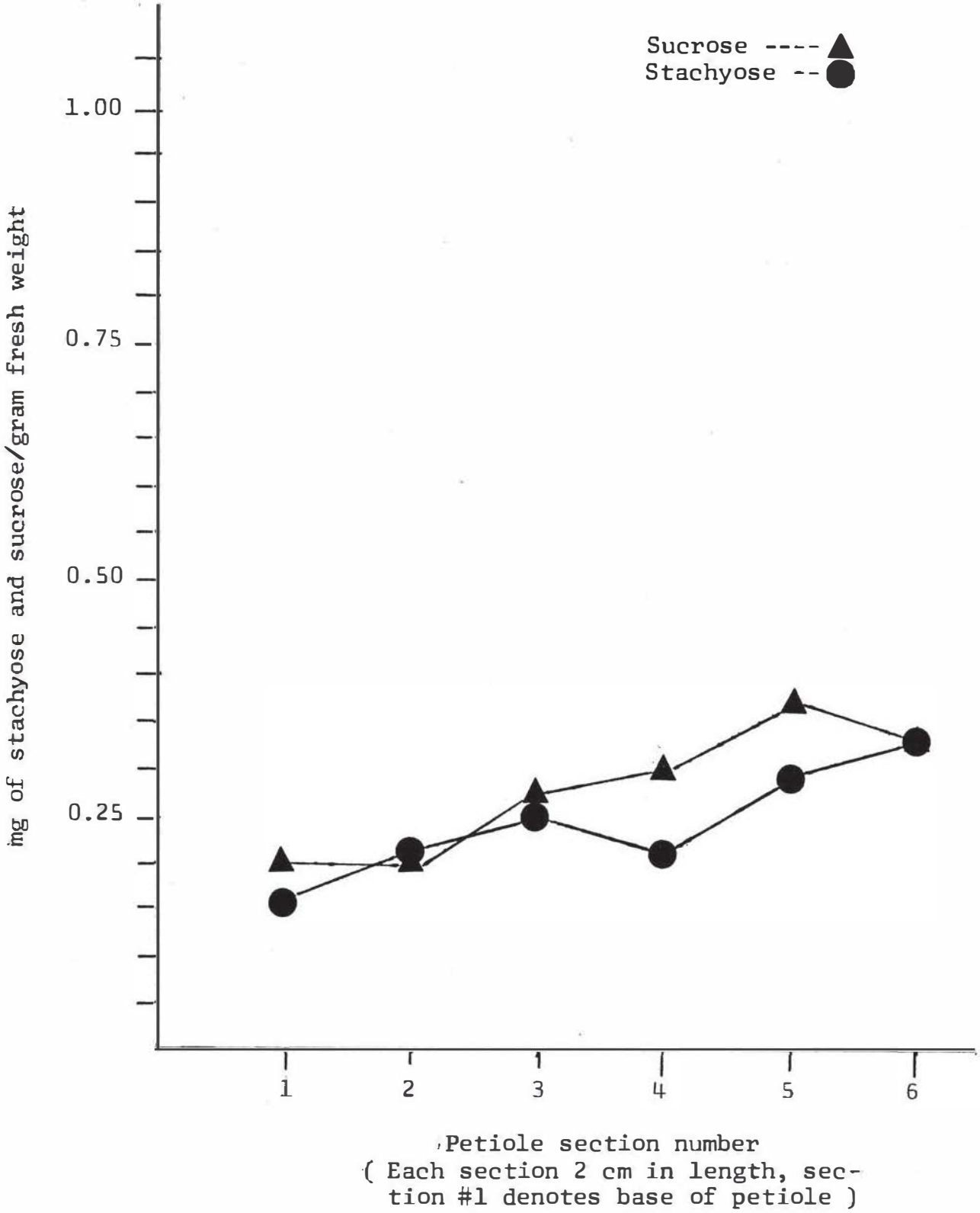
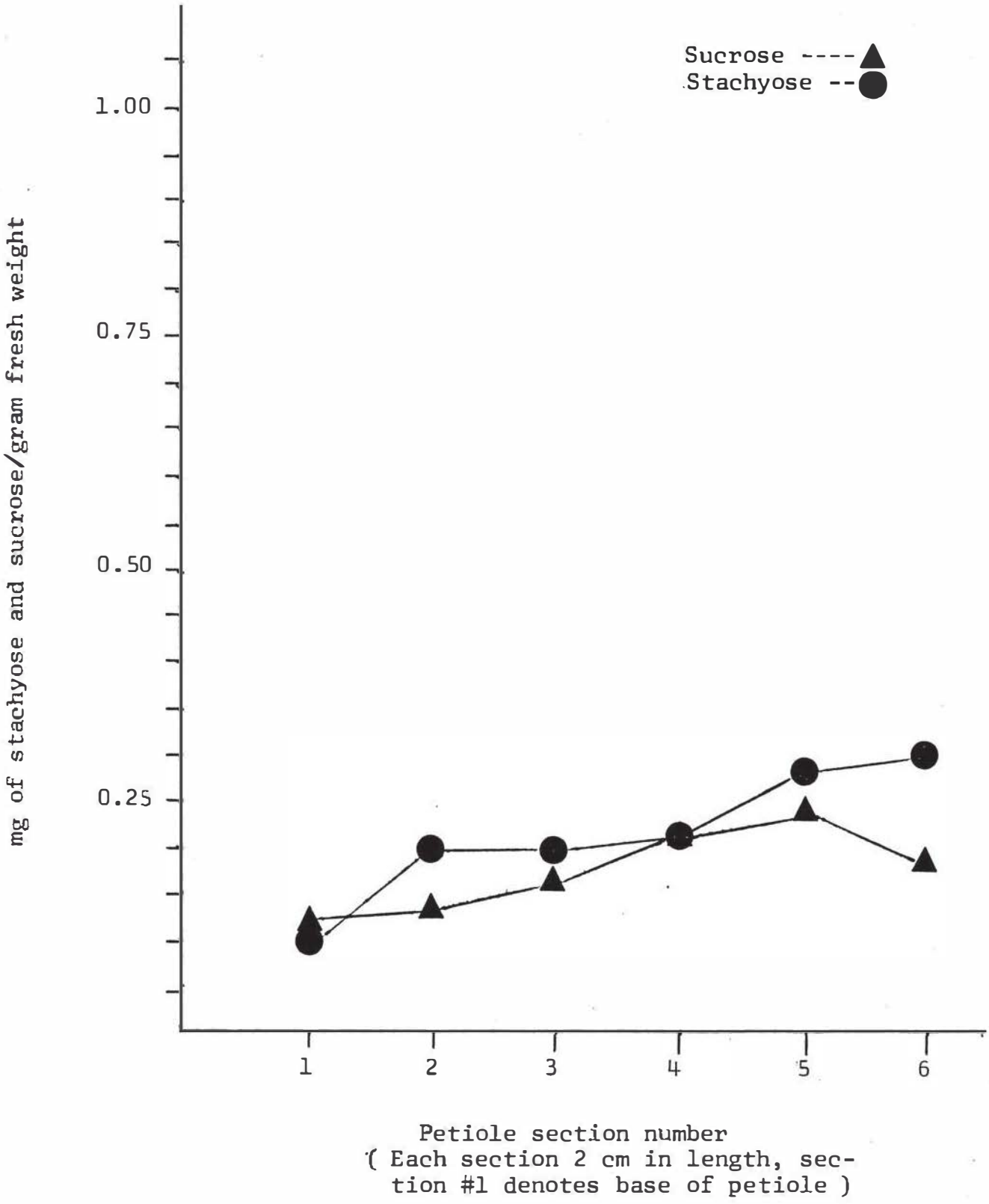

Sucrose ----
Stachyose --
1.00
0.75
0.50
0.25
mg of stachyose and sucrose/gram fresh weight
1
2
3
4
5
6
Petiole section number
(Each section 2 cm in length, section #1 denotes base of petiole)

Fig. 6 Concentrations of stachyose and sucrose in 2-cm sections at 150 minutes after the begining of the dark period.


Sucrose ----
Stachyose --
1.00
0.75
0.50
0.25
mg of stachyose and sucrose/gram fresh weight
1
2
3
4
5
6
Petiole section number
(Each section 2 cm in length, section #1 denotes base of petiole)

dark are compounds that were stored in the leaf and are being converted back into sugar for translocation. Thus, as there is an increase of time into the dark period, there is a decrease in the amount of sugar being translocated.

Figure 7 shows a decrease of stachyose over the four experimental time periods. The rapid decrease in stachyose at 30 minutes may have been due to the generally poor physiological condition of the three experimental plants used for these data. Figure 8 illustrates the gradual decrease of sucrose over the four experimental time periods. The 30 minute slope is also unexpected in this graph, thus supporting the conclusion about the generally poor physiological condition of the plants used for this period.

Discussion

As photosynthetic products are produced many are translocated out of the leaf. At the termination of the light period, and as time increased into the dark period, there was an overall decrease in the amount of total sugar present in the petiole. During the dark period, stachyose and sucrose concentrations dropped off steadily, as expected, but sucrose concentration generally was higher than that of stachyose and declined more rapidly. It would be interesting to know whether both sugars were being translocated

Fig. 7 Fluctuation in stachyose concentration over four periods of time after the begining of the dark period.

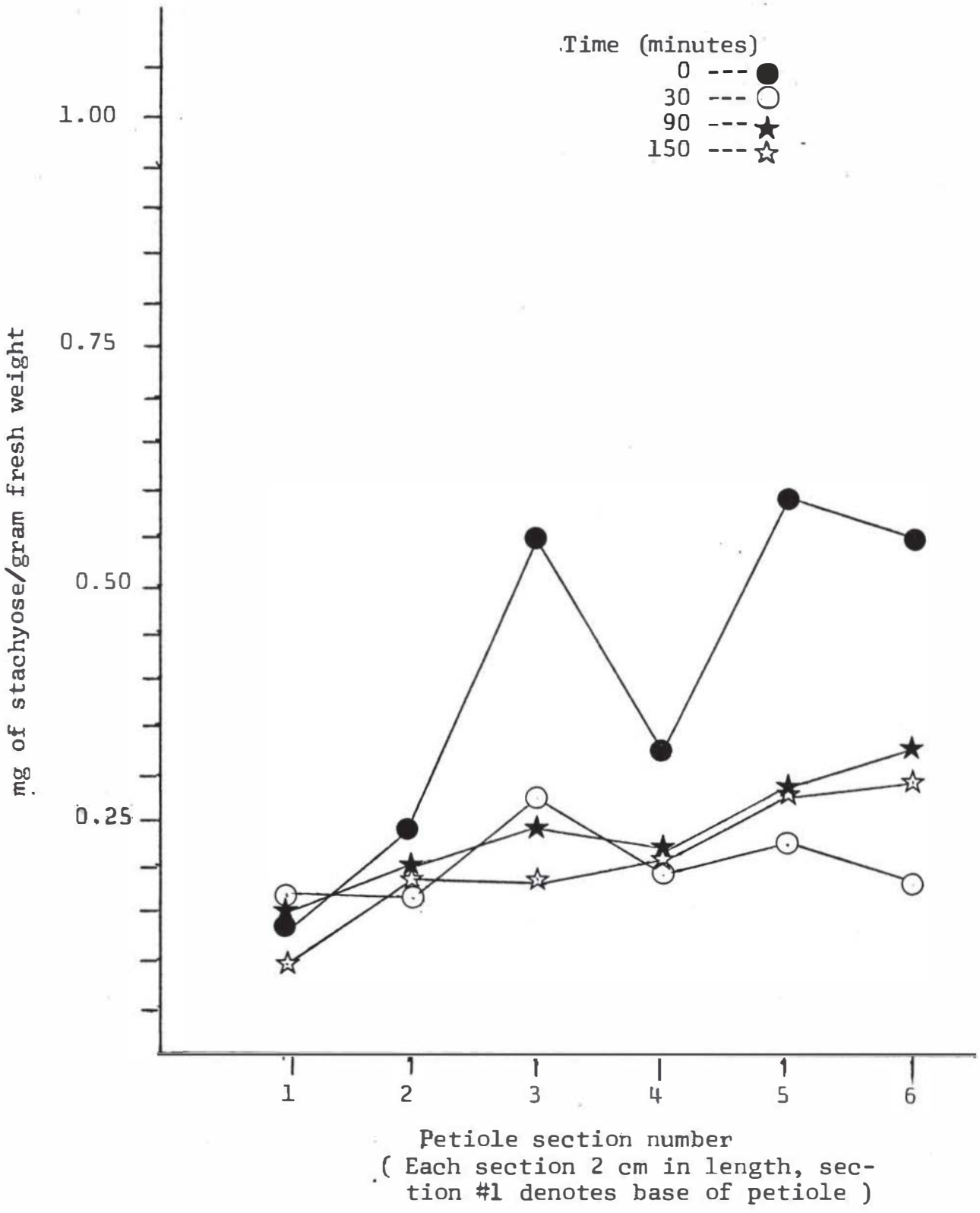
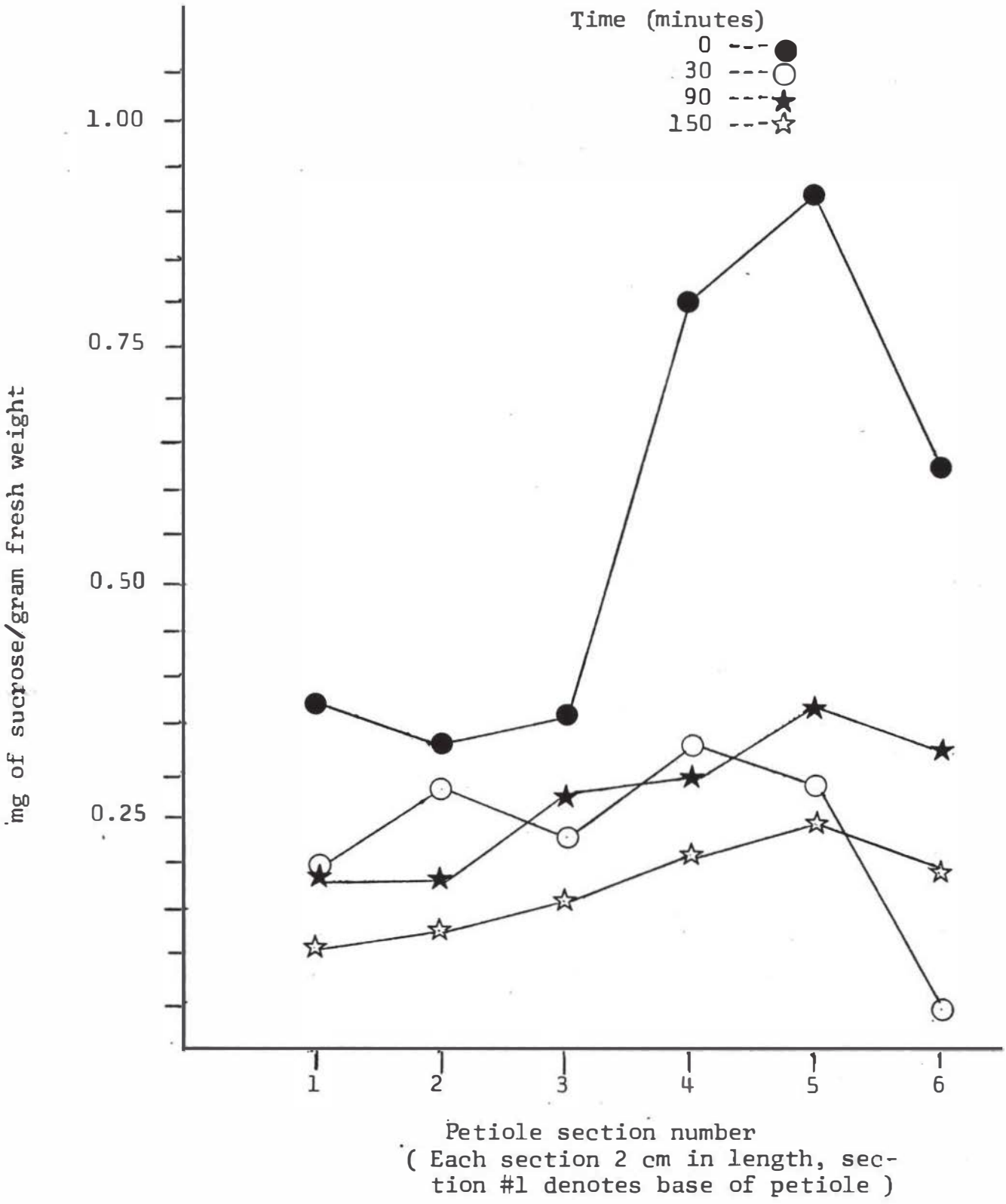

Time (minutes)
0 ---
30 ---
90 ---
150 ---
1.00
0.75
0.50
0.25
mg of stachyose/gram fresh weight
1
2
3
4
5
6
Petiole section number
(Each section 2 cm in length, section #1 denotes base of petiole)

Fig. 8 Fluctuation in sucrose concentration over four periods of time after the begining of the dark period.


Time (minutes)
0
30
90
150
1.00
0.75
0.50
0.25
mg of sucrose/gram fresh weight
1
2
3
4
5
6
Petiole section number
(Each section 2 cm in length, section #1 denotes base of petiole)

simultaneously out of the leaf. There is the possibility that sucrose was being translocated out of the leaf and that stachyose was being translocated into the leaf. The leaf at node 5 during these experiments was a comparatively young leaf. Webb and Gorham (21) have cited experimental evidence which indicates that immature leaves are unable to produce stachyose due to a lack of developed metabolic pathways and are able only to produce sucrose in any sizable quantity. If this is true, perhaps what is being recorded in the data obtained is a simultaneous bidirectional movement of sucrose out of the leaf and the incororation of stachyose into the leaf from more mature leaves which are producing an excess of stachyose. Such evidence, if verified, could be used to refute the theory of mass flow. The data collected during this study cannot be used to support the protoplasmic streaming hypothesis but may add evidence which in the future could be used in its support.

A further extension of this experiment could involve a study of sugar concentration over the full 8-hour dark period to see if there is a complete leveling off of individual sugar concentration of sugar translocated. In addition, work could be done using leaves of varying maturity to observe the relationship of age with the concentrations of stachyose and sucrose being translocated through the petiole.

Summary

The effects of exposure to darkness in straight-neck squash (Curcurbita melopepo torticolis, Bailey) on sugar translocation was studied. The plants were grown on an aerated mineral solution for 21 days in a growth chamber with an alternating 16-hour light period and an 8-hour dark period. On the twenty-first day, at 0, 30, 90, and 150 minutes into the dark period the petioles from node 5 from three different plants were removed. Each petiole was cut into 6 or 7 2-cm sections which were weighed to the nearest 10^{-2} gram and were extracted in a soxhlet extractor for 3 hours. The total sugar present in each extract was determined colorimetrically by the sugar specific anthrone test.

Stachyose and sucrose are considered the main transport molecule and the fluctuations in their concentrations during the dark period was studied. Raffinose, a less prominent translocated sugar, was also studied. Determination of the sugar concentration in each sample was accomplished by paper chromatography which facilitated sugar separation. The portions of the chromatograms containing stachyose, raffinose, and sucrose were eluted with water and sugar determinations were again determined by the anthrone test.

Results indicate that as time progressed into the dark period there was a gradual decrease in the total amount of

in the total amount of sugar present in the petiole. Sucrose was present in higher concentrations than stachyose throughout the four experimental time periods. Both stachyose and sucrose decreased in concentration as the time in the dark period increased. Since a relatively young leaf was used it is suspected that there may have been a simultaneous export of sucrose out of the leaf and the simultaneous import of stachyose into the leaf. Such evidence, if verified could be used to refute the theory of mass flow. Further studies in this direction would possibly lend evidence to support bidirectional translocation and, possibly the protoplasmic streaming hypothesis of carbohydrate translocation.

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