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THE SPATIAL DISTRIBUTION OF CARBOHYDRATES IN THE LEAVES OF MAIZE GROWN IN VARIOUS LIGHT-DARK CYCLES

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Abstract

The distribution of soluble sugar and starch contents was studied according to leaf stages in the leaves of 36 day old maize. The carbohydrate content of plants grown in 16 hr light and 8 hr dark (16—8 hr LDC) control illumination was compared to the values of plants grown in 30—15 min and 15—7.5 min short LDC-s. The changes in the dry mass of the plants were also evaluated.

Adaptation to the short LDC-s manifested in the decrease of the root-leaf dry mass ratio, probably corresponds to the increase in the ratio of the starch per soluble sugar content of the leaves. From the leaf stages, in the short LDCs the dry mass of the 1st and 2nd leaf, and in the 30—15 min LDC even the starch content, increased compared to the control 16—8 hr LDC.

The dry mass of the developed, still intensively photosynthesizing 3rd and 4th leaf was lower in the short LDCs. The considerable decrease observed in the carbohydrate content of these leaves may be in connection with the fact that these leaves have great role in the photosynthetic supply of the youngest 6th leaf, thus the dry mass of the 6th leaf even slightly increases in the short LDC-s and even its carbohydrate content decreases only to a little extent.

The water soluble sugar content of the less photosynthesizing part of the 4th leaf: the midrib and the leaf sheath showed considerable decrease in the short LDC, therefore this is presumably the depository which most likely becomes empty in the case of deficient photosynthate supply.

No difference in soluble sugar content was seen between the base and apex of the leaf lamina, however, the starch content of the leaf base was higher than that of the leaf apex. Difference between these lef parts were not observable on the effect of the short LDC-s.

Key words: water soluble sugar and starch content, short LDC, distribution of carbohydrates maize, leaf stages, leaf parts.

Introduction

One of the important modes of adaptation of plants to changing environmental conditions is the modification of the distribution of the primary products of photosynthesis, the carbohydrates, within the plants, as well as the transformation of the proportional ratio of the various carbohydrate forms (sugar, starch, cellulose).

SCHULZE et al. (1983) studied the increase in biomass of *Vigna unguiculata* plants using the method of mathematical modelling. They have determined that the balance of the growth of the shoot and the root is attained through the changes of the carbohydrate partitioning namely in the function of transpiration and the water absorb capacity of the root.

During the course of adaptation to weaker light intensity the partition into shoots of the photosynthates becomes intensified and thus the shoot/root dry mass ratio, i.e. the ratio of the photosynthesizing/non-photosynthesizing organs increases (BJÖRKMAN, 1982).

On the basis of the studies by CHATTERTON and SILVIUS (1980) the length of the light period also influences the accumulation of photosynthetic starch in the leaf: in the case of shorter light period the accumulation is of higher degree. The distribution of carbohydrates is further influenced not only by the environmental factors but also by the internal demands of the plant which change during the course of ontogenesis. For example, the growth rate of the intensively growing so-called "sink" leaves have influence the carbohydrate level of the older, so-called "source" leaves feeding them (BARLAW and BOERSMA, 1976).

At the time of crop formation the increased photosynthate demand causes the increase of starch accumulation in daylight and its mobilization at night in the photosynthesizing leaves (HAMMOND and BURTON, 1983).

Therefore, the accumulation of photosynthetic starch in the leaf does not serve as the storer of excessive carbon, but it is regulated by complicated control mechanisms according to the demands of the plant and the changes of the environment (HUBER, 1983).

The light-dark cycles varying from thet natural are generally unfavourable to the development of the plant and the increase in dry matter (SAGER and GIGER, 1980), i.e. they mean considerable stress on the plant. Nevertheless there are such period lengths also, where — at least in the case of certain plant species — increase in dry mass is observable in the case of identical daily amount of light compared to light-dark cycles (LDC-s) of natural length (GARNER and ALLARD, 1931; GAUDILLIÉRE, 1977; HORVÁTH et al., 1977; MARÓTI and MIHALIK, 1983).

Adaptation to short light-dark cycles can be expected in the changes of carbohydrate distribution, partly in the changes regarding the ratio of soluble sugars and starch compared to each other, as well as in the changes in the distribution of carbohydrates between leaves of various ages and also in the different parts of one particular leaf.

Based on earlier studies, the soluble sugar, starch and cellulose contents of the 5th leaves (counted from the bottom of 5-week-old maize) were enhanced or reduced depending on genotype in the 30—15 min. LDC. The 15—7,5 min LDC, however, strongly decreased the soluble sugar and starch contents of the 4th and 5th leaves in the case of every genotype, while the cellulose content [μg mg^{-1}] was increased (dry mass, mg/leaf) (MARÓTI and MIHALIK, 1983). We have no data on how the carbohydrate content of the older (1st—3rd) and the youngest (6th) leaves changes compared to the central leaves, furthermore, on how the carbohydrate content changes on the effect of short LDCs in the various parts of one single leaf. The relationship between the changes observed in carbohydrate content and dry mass of the plant organs is still to be studied. In the present paper answer is sought to the above questions studying 36 days old individuals of P3732 and P3839 hybrid maize.

Materials and Methods

In our experiments 3732 and 3839 Pioneer maize hybrids were used. The maize grains were sown in the mixture of washed sand-perlite in the ratio of 1:1. The moisture and nutriment content of the growing medium was ensured by mixture with Hoagland nutrient solution (REYSS and BOURDU, 1971) modified by BÉRCZI et al. (1982) and MARÓTI. The macroelement content of the nutrient solution was as follows: K^+ (3 mM), Na^+ (0.4 mM), Ca^{2+} (5 mM), Mg^{2+} (0.4 mM), NO_3^- (12 mM) Cl^- (1 mM), HPO_4^{2+} (0.2 mM), SO_4^{2-} (0.4 mM) per dm^3. The microelement content was: BO_3^{3-}

(1.6 mM), Mn^{2+} (0.8 mM), MoO_4^{2-} (0.05 mM), Zn^{2+} (21.8 µM), Cu^{2+} (25.1 µM) per dm^3. The moisture content of the medium was set to the value of water capacity corresponding to 80%. The original moisture content was maintained daily with tap water by watering according to weight. The pH ranged from 7.4 and 8.2 in the medium.

In a plastic pot with volume of 600 cm^3 5 maize grains were sown 4—5 cm deep. At the age of two weeks the plant numbers were changed to 3 per dish. Nutriment was supplied twice a week: with 20 ml of above described nutrient solution per pot. The plants were grown in phytotron (HORVÁTH, 1972). In the climate chambers the temperature was 21 ± 2 °C, the relative moisture content of the air was 50—70%. The CO_2 concentration was kept on the same level by constant mixing with fresh air. F29 and F33 light tubes were used for illumination. The strength of illumination in the light phase was 32 Wm^{-2} (= 185 $\mu Em^{-2}s^{-1}$).

Three kinds of light treatment were applied: The alternation of 16 hours light and 8 hours dark was used in the first climate chamber (16—8 hr LDC). The light phase lasted from 8 a.m. till midnight. In the second climate chamber 30 min light and 15 min dark (30—15 min LDC) and in the third 15 min light and 7.5 min dark (15—7.5 min LDC) alterated continuously.

The duration of the daily total illumination was 16 hours in all three chambers, thus the daily total radiating energy was 1843 kJm^{-2}.

Two experiments were carried out: the individual number was 15 per chamber in the first and 9 in the second.

The carbohydrate content was determined on 9—9 plants from the second experiment.

The plants were processed at the age of 36 days, during the hours before noon. From the short LDC-s the samples were taken during the light phase according to organs and leaf stages. The separated plant matter taken from the 4th leaf of the P3839 hybrid according to leaf parts (leaf base — centre — apex) was fixed at 105 °C for 5 min and then dried for 10 days at 60 °C. Then dry mass was measured on analytical scale. The carbohydrate content was determined from the pulverized dry matter. The soluble sugar was extracted twice with hot water. The starch was extracted from the sediment with perchloric acid according to the method of MCCREADY et al. (1950). The sugar content of the extracts was measured with the phenol-sulphuric acid method of DUBOIS et al. (1956) and determined with the aid of comparative solution prepared from glucose from the extinction values. (For detailed description of the method see: MARÓTI and MARGÓCZI, 1984).

The results were statistically evaluated: the significance of the variations in values obtained from the 16—8 hours control LDC and the two short LDC-s was determined with the help of the t-probe. In the Tables and graphs the significance appears as follows: P=10%*, P=5%**, P=1%***, P=0.1%****.

Results

1. THE EFFECT OF SHORT LDCs ON THE DRY MASS OF 36 DAYS OLD MAIZE PLANTS

In 3732 hybrid maize the dry mass of each organ decreased on the effect of short LDCs at the age of 5 weeks. The total dry mass showed a decrease in the 30—15 min LDC compared to the 16—8 hr LDC, and even further decrease was experienced in the 15—7,5 min LDC (Table I).

Table I. Dry mass of the various organs of P3732 hybrid maize at the age of 36 days in normal and short LDCs [mg/plant], and the proportional quota of the organs from the total dry mass. The data are the average values of 24 plants. The significance of the variation from the values of the 16—8 hr LDC is demonstrated according to the description in Materials and Methods.

LDC	Dry mass							
	root		leaf sheath		leaf lamella		total	
	mg	%	mg	%	mg	%	mg	%
16—8 hour	657.8	46.9	246.6	17.6	497.4	35.5	1402.0	100
	*							
30—15 min	504.1	45.0	160.7	15.2	446.5	39.8	1111.3	100
	***		*					
15—7.5 min	431.9	41.9	181.6	17.6	418.2	40.5	1031.6	100

The dry mass decreasing effect of the short LDCs was of various degree in the organs of the plants. The dry mass decreased the most in the root, and the least in the leaf, therefore the organ-ratios changed in the short LDCs. The quota of the dry mass in the root decreased from the total dry mass and that of the leaf showed an increase (Table I).

The length of the leaf sheaths increased in the short LDC, but their thickness decreased. (In the 36 day old plants the leaf sheaths play role as the stem. The initiatives of the young leaves are protected by the cob formed by the older leaf sheaths. In our paper this stem-like organ: the initiatives of the young leaves and the older leaf sheaths protecting them, are jointly named as the leaf sheath). Due to the two kinds of proportion changes, in the 30—15 min LDC the decrease in dry mass of the leaf sheaths refers to the fact that the decrease in thickness prevails in this part of the plant, while in the 15—7.5 min LDC, due to the organ's vigorous increase in length, its dry mass decreased less as in the 30—15 min LDC, and its quota from the total dry mass is the same as in the control 16—8 hr LDC.

2. Changes in dry mass of the leaf stages in short LDC

At the time of harvesting the plants were in six-leaved state. The 1st, lowest leaf was strongly dry, the 2nd leaf was less dry. The lingule of the 3rd and 4th leaves already appeared, therefore they were considered to be completely developed leaves. The 5th leaf was of significant size, but was still intensively growing. The 6th leaf appeared 3—5 cm from the cob formed by the leaf sheaths. (Dry mass measurement and carbohydrate determination were only performed from this 3—5 cm part).

During the course of the experiments it was observed that the lingule of the leaves appeared 1—1.5 days earlier in the short LDCs than in the control 16—18 h LDC. In the short LDCs the degree of withering was lower in the case of older leaves. The short LDCs had various effects on the different aged leaves of the plants. In the 30—15 min LDC the increase in dry mass of the 1st and 2nd leaves reached 20% compared to the control 16—8 h LDC, but in the 15—7.5 min LDC it was also 10% (Table 2). In both short LDCs the dry mass of the 3rd, 4th and 5th leaves decreased; strongly that of the 4th leaf, less that of the 3rd and 5th leaves. The dry mass of the 6th, youngest leaf only slightly increased in the short LDCs (Table 2).

Table II. Dry mass of the leaf lamellae of P3732 hybrid maize at the age of 36 days in normal and short LDCs [mg/leaf]. The leaf stages were counted from the bottom. The data represent the averages of 24 plants

LDC	Dry mass [mg/leaf]						
	Leaf position	1.	2.	3.	4.	5.	6.
16—8 hour		13.2	34.0	92.2	179.0	139.3	39.6
30—15 min		15.9	41.4	82.5	137.9	127.6	41.6
15—7.5 min		14.4	37.2	74.1	126.4	126.0	40.1

3. Carbohydrate content of the leaves

3.1. *The water soluble sugar content* (Fig. 1):

In the 16—8 hr LDC the water soluble sugar content of the leaves referring to dry mass unit developed as follows: it was found to be relatively high in the old 1st and

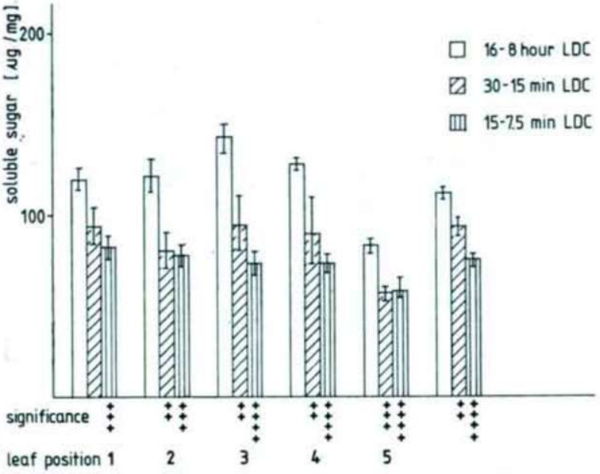

Fig. 1. The development of the water soluble sugar content in each leaf stage of P3732 hybrid maize in control and short LDCs, referred to dry mass unit (μgmg^{-1}). The data are the average values of 9—9 35 days old plants. The significance of the variation from the data of the 16—8 hr control LDC is demonstrated according to the description in Materials and Methods. The leaves counted from the bottom upwards.

2nd leaves, and was the highest in the developed 3rd and 4th leaves. Strikingly low amount of water soluble sugar was found in the 5th leaf — growing intensively, but already having larger area than the 4th leaf — and again somewhat higher amount was found in the 6th leaf. The difference in water soluble sugar content between the leaf stages became moderate in the short LDC. These differences almost disappeared in the 15—7.5 min LDC, only the low soluble sugar level of the 5th leaf was striking. More or less equal amount of water soluble sugar was found in the rest of the leaves, per unit dry mass.

3.2. *Starch content* (Fig. 2):

In the 16—8 hr LDC the starch level referring to dry mass unit was similarly high in the 4th, 5th and 6th leaves. It was rather low in the old, 1st leaf, and in the 2nd and 3rd leaves the starch content was found to be between the two above mentioned values. Namely, the starch level increased from the 1st to the 4st leaf. The starch level of the leaf stages compared to each other showed strong modification in the 30—15 min LDC: that of the 1st leaf was also relatively low here, but was still higher than the equivalent data of the 16—8 hr LDC.

The starch level of the 2nd leaf was strikingly high, from here it decreased till the 3rd, 4th leaves, increasing again in the 5th and 6th leaves.

Similar tendency was observed in the 15—7.5 min LDC with the difference that here an increase in starch level could not be experienced even in the 1st and 2nd leaves compared to the adequate data of the 16—8 hr LDC.

As a summary therefore, it could be concluded that the short LDCs only decreased the soluble sugar content of the lower 1st and 2nd leaves, the starch content even increased in these leaves on the effect of the 30—15 min LDC. Both the water soluble sugar and starch levels strongly decreased in the 3rd and 4rd leaves. In the

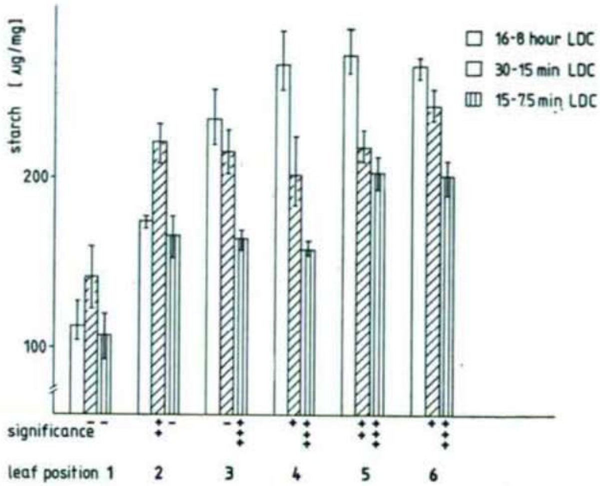

Fig. 2. The development of the starch content in each leaf stage of P3732 hybrid maize in control and short LDCs, referred to dry mass unit (μgmg^{-1}). The data are the average values of 9—9 35 days old pants. The significance of the variation from the data of the 16—8 hr control LDC is shown according to the description in Materials and Methods. The leaves were counted from the bottom upwards.

5th leaf the decrease was somewhat slighter and in the 6th leaf the decrease of carbohydrate content was even more moderate in short LDC.

Studying the percental share of starch from the total carbohydrate content, a continuous increase in starch proportion could be observed from the older leaves to the younger ones in each LDC, with the exception of the youngest leaves where the proportion of starch was found to be lower than in the previous leaf stages (Table 3).

Table III. The carbohydrate content referring to dry mass unit of the leaf lamellae of P3732 hybrid maize: water soluble sugar+starch: Su+St [µg/mg] and the quota of starch from the total carbohydrate content: St%. The data are the averages of 9—9 plants. The leaf stages were counted from the bottom.

LDC		Leaf position					
		1.	2.	3.	4.	5.	6.
16—8 hour	Su+St [µg/mg]	233.1	296.3	376.2	393.3	355.6	376.8
	St%	48.7	58.9	62.2	67.6	76.6	70.5
30—15 min	Su+St [µg/mg]	244.9	300.3	309.6	290.9	275.9	335.8
	St%	61.9	73.5	69.5	69.3	79.2	72.1
15—7.5 min	Su+St [µg/mg]	189.9	244.2	238.4	249.9	261.5	274.6
	St%	56.6	68.1	69.1	71.2	78.8	73.0

Comparing the effect of the various LDC treatments for each leaf stage, it could be seen that the proportion of starch always increased in the short LDCs. In general, there were no great differences in this regard between the two short LDCs (Table 3).

4. THE CARBOHYDRATE CONTENT IN THE VARIOUS PARTS OF THE 4TH LEAF (Figs. 3—4)

This experiment was carried out on the 4th, leaf of 36 days old P3839 hybrid maize plants. The carbohydrate content per dry mass unit was determined separately in the leaf sheath, midrib and the base, center and apex of the leaf lamella. The results showed that in the 16—8 hr LDC there were no differences between the various

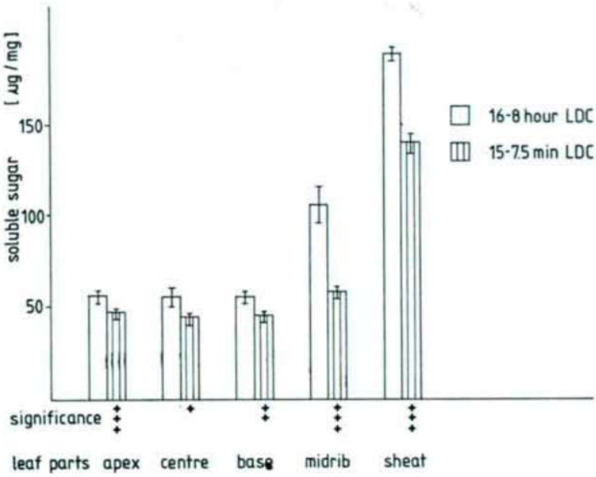

Fig. 3. The development of the soluble sugar content in the various parts of the 4. leaf of P3839 hybrid maize in 16—8 hr and 15—7.5 min LDCs, referred to dry mass unit ($\mu g mg^{-1}$). The data are the average values of 9—9 35 days old plants. The significance of the variation from the data of the 16—8 hr LDC is demonstrated according to the description in Materias and Methods.

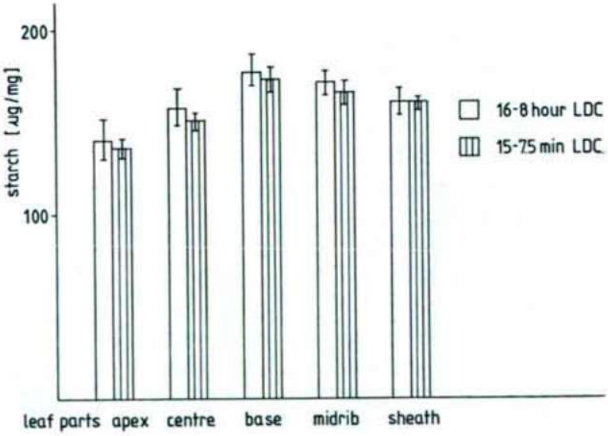

Fig. 4. The development of the starch content in the various parts of the 4. leaf of P3839 hybrid maize in 16—8 hr and 15—7.5 min LDCs, referred to dry mass unit ($\mu g mg^{-1}$). The data are the average values of 9—9 35 days old plants. The variations from the data of the 16—8 hr LDC did not prove to be significant in this experiment.

parts of the leaf lamella in respect to the soluble sugar content. The soluble sugar content of the midrib was almost the double of the sugar content of the leaf lamella and that of the leaf sheath was even higher (Fig. 3). On the effect of 15—7.5 min LDC the soluble sugar level of the leaf lamella only slightly decreased, however, the decrease was about 40% in the midrib, and 25% in the leaf sheath. In the leaf lamella the starch content increased from the apex to the base both in the 16—8 hr and 15—7.5 min LDCs. The starch content was considerable in the midrib and sheath of the leaf. On the effect of short LDC the starch content decreased slightly but not significantly in the various parts of the leaf lamella and in the midrib, but showed no changes in the leaf sheath (Fig. 4).

Discussion

Since both the dry mass and carbohydrate content/dry mass unit of the plants decreased (Tables 1, 3) it could be concluded that in short LDCs there is a decrease in the daily gain of CO_2, i.e. in the net photosynthesis. Though in the short LDCs the plants received the same amount of daily light (1843 kJm^{-2}) as in the 16—8 h control LDC, the repeated, compulsory adaptation due to the frequent light-dark-light transition in the short LDCs hinders the more complete utilization of the light. That is, the plants "starve" in the short LDCs, the same amount of light used in short periods seems to be less for the plant, being less able to utilize it in the formation of carbohydrate. Therefore, it is compelled to ensure the relatively optimal growth by modifying the distribution of the photosynthates as described in the followings.

On the one hand the ratio of the photosynthesizing and nonphotosynthesizing organs changes to the benefit of the photosynthesizing leaves (Table 1). This was also concluded by BJÖRKMAN (1982) in the case of applying weaker light intensity compared to the stronger one.

Regarding the modification of the organ-ratio, such a mechanism may play role which is effective on the growth of the root through influencing the starch level of the leaf. In our case the decrease in the root proportion observed in the short LDCs may be in relationship with the increase in the ratio of starch/soluble sugar. This assumption is in conformity with the results of HUBER (1983), who found connection between the higher starch/sugar ratio and the lower root/shoot dry mass ratio of the leaf in plants having various genotype and nitrogen supply.

The changes in phosphoglyceric acid and inorganic phosphate level of the chloroplast — through the phosphate translocator — may possibly play role in the regulation (WALKER, 1976; PREISS, 1982).

The photosynthetic starch accumulation-reducing effect of the plant's temporary increased photosynthate demand — which appears in the greater saccharose translocation — is realized through this system. However, not every link has been clarified as yet regarding the path leading from the changes of environmental factors to the accommodation the biochemical metabolism of the cell. The temporary photosynthate demand is probably not the only influencing element of the photosynthetic starch accumulation, as in such case the lower starch/sugar ratio of the leaf should have been found in the short LDCs.

In our experiment the leaves of various ages behaved differently on the effect of short LDC.

The dry mass of the lower (1st, 2nd) leaves was found to be higher in both short LDCs than in the control LDC (Table 2), and the starch content was also higher in the 30—15 min LDC (Fig. 2). These leaves developed when the reserve nutriment of the germinating seed still strongly contributed to the development of the plant, i.e. the nutriment flow from the seed probably compensated the decreased CO_2 gain in the short LDC. It is of interest that the high starch content observed in the 1st ans 2nd leaves in the 30—15 min LDC refers to the fact that these leaves did not even completely "empty" at the time when newer leaves grew.

In all probability the considerable decrease in the soluble sugar and starch content of the no longer growing, but still intensively photosynthesizing 3rd and 4th leaves makes it possible that the dry mass of the 6th leaf even increases to a certain extent in the short LDC, and the carbohydrate content only slightly dec reases (Table 3). This observation is in accord with the results of BARLAW and BOERSMA (1983), according to whom there is relationship between the growth rate of the young leaves and the carbohydrate level of the older leaves feeding them.

Similarly to the results of MILFORD and PEARMAN (1975), CHANG (1979), and POTTER (1980), in our experiment it was found that the proportion of starch was higher in the total extracted carbohydrate in the younger leaves than in the older ones (Table 3).

Since the short LDC increases the proportion of starch at identical leaf stages (Table 3), we can presume that this also means the retardation of the aging the leaf. This is further referred to by our observation that in the short LDC the lower leaves wither later than in the 16—8 hr LDC.

On studying the carbohydrate content of the leaf parts it was determined that the proportion of starch decreases from the base towards the apex (Fig. 3, 4). The differences in age of the three leaf parts are presumably reflected in this: the basal part is the youngest, the leaf apex is older. PERCHOROWICZ and GIBBS (1980) found difference between the basal and apex parts of maize leaves regarding the explicity of the C4 features. The carbohydrate content in all three parts of the leaf lamella decreases to the same extent on the effect of short LDC (despite the differences in age). Compared to the photosynthesizing part of the leaf lamella rather considerable decrease can be observed in the soluble sugar content the midrib of the leaf and leaf sheath on the effect of short LDC. This may refer to the fact that the depository best available for the younger leaves in case of deficient photosynthate supply is firstly the soluble carbohydrate content of the less photosynthetic part of the 4th leaf, having main role in the photosynthate supply of the young leaves.

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