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ANATOMICAL COMPARISON OF THE FLAG AND SECOND LEAVES OF TWO TRITICUM AESTIVUM CV. SPECIES

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Abstract

The anatomical structure of flag and second leaves of two autumn wheats: *T. aestivum* cv. GK Szeged and cv. Jubilejnaja 50 was studied by light- and with scanning- electron-microscopy (SEM). One part of the plants were grown in the glass house, the other part grew in arable land.

The flag leaves of both wheat cv. were slightly thicker, wider, their area larger, and contained cc. 20 larger and smaller intermediate bundles more than the second leaves. Compared to the second leaves, the width and thickness of the GK Szeged flag leaves, and the length and area of the Jbj 50 flag leaves were significantly larger.

On the abaxial side of the GK Szeged and Jbj 50 cv. flag leaves, above the small intermediate bundles and between the veins, the height of the mesophyll cells was smaller than in the second leaves. In the flag leaves the height of the mesophyll cells beneath the bulliform cells decreased in the case of Jbj 50, and showed almost no changes in GK Szeged, compared to the second leaves.

As a uniform characteristic, in the two wheat types the multilobed cells were more frequent in the flag leaves than in the second ones. In both leaves of Jbj 50 the multilobed mesophyll cells occurred in higner percentage than in the leaves of GK Szeged.

The flag leaves of both wheats had significantly higher number of stoma and trichoma and stronger epicuticular wax covering on the adaxial than on the abaxial surface.

On the basis of the alterations in the lobed structure of the mesophyll cells and our previous studies it is assumed that in the chloroplasts of flag leaves the ratio of cyclic per linear electron transport is higher than in the chloroplasts of the second leaves.

Key words: *Triticum aestivum*, flag and second leaves, morphology, lobed mesophyll cell, epidermis.

Introduction

In the recent years sereval authors (CHONAN, 1965, 1966, 1970; KHAN and TSUNODA, 1970, 1971; AUSTIN et al., 1982; PARKER and FORD, 1982) demonstrated reaationship between the anatomical structure and photosynthetic activity of wheat leaves. The majority of the authors (KHAN and TSUNODA, 1970; EVANS and DUNSTONE, 1970; AUSTIN et al., 1982; PARKER and FORD, 1982) connect the intensity of photosynthesis with the larger surface of the leaves in the case of wheat, too, which — according to these authors — facilitates the diffusion of carbon dioxide into the mesophyll cells.

The question is how the larger internal surface and more intensive carbon dioxide uptake of the diploid *T. urartu* leaves could be fit together with the larger productivity of the hexaploids.

AUSTIN et al. (1982) isolated chloroplasts and protoplasts from diploid, tetraploid and hexaploid wheat leaves and demonstrated that the ratio of the light-dependent oxygen evolution was close to similar. Authors assumed that the differences in photosynthesis between the intact leaves may originate from the anatomical variations of the leaves. On the basis of the studies on the genotype of 15 diploid, tetraploid and hexaploid wheats, authors did find positive relationship between the vein density and maximum photosynthetic rates.

This observation also calls attention to the intensity in transport of the assimilates. The question arises, however, whether the higher amount of assimilates are transported because there are more veins, or because a larger number of assimilates develop, which are capable of transport and vein-formation, resp.

Opinions vary regarding the place of formation of the organic matter accumulated in the yield and the rate of participation of certain organs. On the basis of his experiments carried out with comparative defoiling, BONSTRA (1937) drew the consequence that from the assimilates found in the grains 75% is produced in the upper part of the wheat: in the spike (34%), the upper internode (12%), the flag leaves (13%) and sheath (16%).

According to the studies of SIMPSON (1968) and FOCKE (1973) in the majority of wheat species the spike shows the tightest connection with the yield, in point of view of assimilate-formation, and this is followed by the flag leaf and the rest of the leaves.

The role of the spike is coming more and more into the foreground with the decrease in the height of the species, while that of the flag leaf and the other leaves is changing according to variety (BEKE, 1977).

According to the studies of NALBORCZYK (1978), in the case of wheat the spike contributes to the development of the total photosynthetic products (dry matter) in 9.3%, the upper internode in 16.2%, the flag leaf lamina in 36.6%, the flag leaf sheath in 7.0%, the lamina beneath the flag leaf in 18.8%, the second leaf sheath in 7.1%, the third leaf and the internode underneath in 4.2%.

On the basis of the studies by LEDENT and POCHET (1978) the length of the veins counted per unit area of the flag leaves, and the number of tracheas, resp. show tighter correlation with the yield than the area, width or weight of the flag leaves.

The questions raised cannot be solved by histo-comparative studies on the flag leaves and leaves under these, but — besides the fact that there are no such studies — indicate the histological examination of the two upper leaves of two hexaploid wheat types having various productivity (Jubilejnaja 50, GK Szeged).

The literary data are in agreement in that the spike has significant role in the formation of assimilates stored in the grains; this is followed by the flag leaf and with great difference, by the second leaf beneath this.

In the present paper we study on one part how this variation is manifested in the tissue structure of the leaves, and on the other part, a new relationship is presumed between the structure of the mesophyll cells and photosynthesis.

Materials and methods

PLANTS AND EXPERIMENTAL CONDITIONS

The experiments were carried out with the autumn types of Triticum aestivum L. commonly cultivated in Hungary; cv. GK Szeged and cv. Jubilejnaja 50. The GK Szeged is a wheat type which is intensive and belongs to the group of early ripening, its largescle productivity is 7.0—8.5 t ha^{-1}. The Jubilejnaja 50 is a wheat type which can be securely cultivated, belonging to the group of moderately early ripening. Its large-scale productivity is 6.0—6.5 t ha^{-1}.

For one of the experiments — to determine the thickness of the flag leaves and second leaves beneath these; the measurements of the mesophyll cells; as well as the lobe number and stoma number and measurements — the two types of wheat were grown in Henssler-type climate-house according to the followings: the two-leaved plants were placed into pots with diameters of 14 cm (4 plants/pot) after 50 days of vernalization and were grown in homogenized soil supplied well with nutriment. Following unpotting the plants grew for 10 days at 13—15 °C under 50—55% relative humidity.

Then the temperature was raised to 21—23 °C and the humidity varied between 60—65%.

The daily 14 h illumination of the plants was ensured by 400 W Phillips HLRG lamps (30 W/m^2) in January, February and March.

For the other experiment — to determine the measurements of the flag and second leaves; the number and density of the bundle types; and the amount and measurements of the stoma — the

wheat plants were grown in the fields, in the Lower ground of the Cereal Research Institute at Szeged. The time of sowing was October 14, 1980, performed with 400 seeds/m² close setting in plots of 10 m².

In case of both experiments the flag and second leaves were collected for anatomical examinations at the time of flowering.

Determination of the measurements of leaf laminae and amount of veins

50—60 plants grown in the fields were taken in order to determine the length, width and area of the flag and second leaves. After the determination of the fresh weight drawings were made from the laminae of the leaves and the area was recorded by weighing.

To determine the type and amount of the leaf veins 1 cm long pieces were cut from the centre part of the leaves (about 12 cm from the base) and these were refined in 5% sodium hypochlorite solution for 24 h, then washed in thin acetic acid. The refined leaves were placed into photographic enlarging apparatus and projected (Fig. 2.)

For labelling the various bundle types the works of Patrick (1972) and Kuo et al. (1974) were applied: the midrib was the largest, followed by the 6 large laterals (Ll), and then the four smaller laterals (Sl). The amount of larger lateral bundles was generally 10 (5 oh one side), among these varrying numbers and sizes of large intermediate (Li) and small intermediate (Si) bundles were found. The leaf laminae thickness was measured in the case of the Ll, Li, Si bundles, and in the direction of the bulliform cells situated in the neighbourhood of these bundles (Llb, Lib, Sib) (Fig. 1).

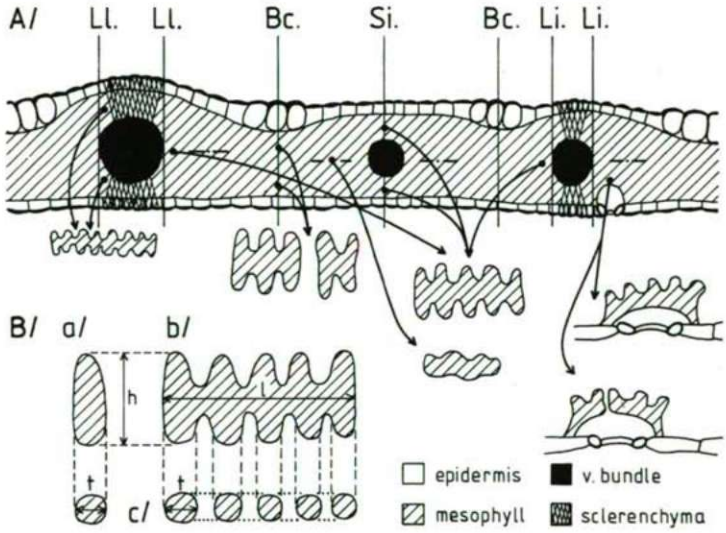


Fig. 1. A) Diagram of the transverse view of the leaf, places of measurings of the height, width (lobe diameter) of mesophyll cells, and longitudinal view of mesophyll cell forms characteristic to the places of measurings (Ll: large lateral; Li: large intermediate; Si: small intermediate bundles; Bc: bulliform cells). B) Transverse (a) longitudinal (b) and top view (c) diagram of the mesophyll cell (h = height of cell; t = cell thickness and lobe diameter; l = cell length).

Studies on the mesophyll cells

For the mesophyll studies samples were taken from the centre part of the flag and second leaves of four plants (about 12 cm from the base). The transverse and longitudinal sections of 25—30 μm were prepared by Leitz Landa type freezing microtome. Zeiss NU_2 light microscope was used for the mesophyll cell measurings.

In the transverse sections of the leaves measurements were taken of the height (h) and thickness (t) (width) of the mesophyll cells. The width of the cells correlated with the diameter of the lobes (Parker and Ford, 1982).

The mesophyll cells were measured at the following points:

1. the large lateral (Ll);
2. large intermediate (Li);
3. small intermediate (Si) bundles and
4. in the direction of the bulliform cells (Bc) situated between them, on the reverse and surface sides, resp. (Fig. 1).

30—30 cells were measured at each point, therefore, a total of 240 cells were measured from the surface and reverse sides.

In the leaf-longitudinal sections the lobes of the mesophyll cells were counted. The length of the cells was not measured, however, this could be calculated from the diameter and number of the lobes. During the course of one of the measurings (without selection) about 200 mesophyll cell lobes were counted. In the case of the other measuring (about 40—50 cells) the lobe number of the mesophyll cells beneath bulliform cells was distinguished.

LIGHT-AND SCANNING- ELECTRON-MICROSCOPIC STUDIES ON THE EPIDERMIS

The 1 cm^2 pieces gained from the centre part of the flag leaves were fixed with so-called Karnovsky solution (KARNOVSKY, 1965) containing paraformaldehyde-glutaraldehyde for a period of 6 h at +4 °C. Then after washing in phosphate buffer (0.1 M pH 7.2) for 18 h the samples were dehydrated linearly in acetone and dried at carbon dioxide atmosphere by critical point method (Polaron).

The dried samples were then studied after gilding in a TESLA BS 300 type scanning-electron-microscope.

In order to measure the amount of stoma and the length of the guard cells excoriations were prepared from the centre part of the leaves. The average of the data of 50 visual fields (M:10×16) per sample was evaluated in the epidermis studies.

Results and discussion

MORPHOLOGICAL CHARACTERIZATION OF THE FLAG AND SECOND LEAVES OF GK SZEGED AND JUBILEJNAJA 50

The flag leaves of both wheats were slightly wider, their area larger than that of the second leaves. The area of the upper two leaves of GK Szeged was larger than those of the Jubilejnaja 50. In the case of both wheat types the length of the flag leaves varied oppositely compared to the second leaves. The flag leaves of GK Szeged were shorter, those of Jubilejnaja 50 were longer than the second leaves (Table 1).

Table 1. Measurements and number of bundles of the flag and second leaves

	GK Szeged flag leaf	2 nd leaf	Jubilejnaja 50 flag leaf	2 nd leaf
Measurements of the leaf:				
Lenght (cm)	25.1±3.2	27.2±2.8	27.6±3.4	25.8±2.6
Width(cm)	2.1±0.3	1.9±0.8	1.8±0.2	1.7±0.2
Area (cm^2)	44.7±5.2	43.6±4.6	41.7±5.1	35.8±3.5
Type of bundles:				
No. of Ll+Sl (No/leaf)	11	10	10	9
No. of Li+Si (No/leaf)	52	32	47	28
Length of Ll+Sl (cm/cm^2)	5.23	5.26	5.55	5.29
Length of Li+ Si (cm/cm^2)	24.76	16.84	26.11	16.47

Types of bundles: Ll large lateral; Sl small lateral; Li large intermediate; Si small intermediate. The measurings are the average data of 50 completely developed (flowering) plants grown in the field. The leaf width means the greatest width.

Great difference could be observed in the number of large and small intermediate bundles and the length per unit surface of the flag and second leaves (Table 1).

In the flag leaves, close to 20 more intermediate bundles were found in case of both wheats than in the second leaves (Fig. 2).

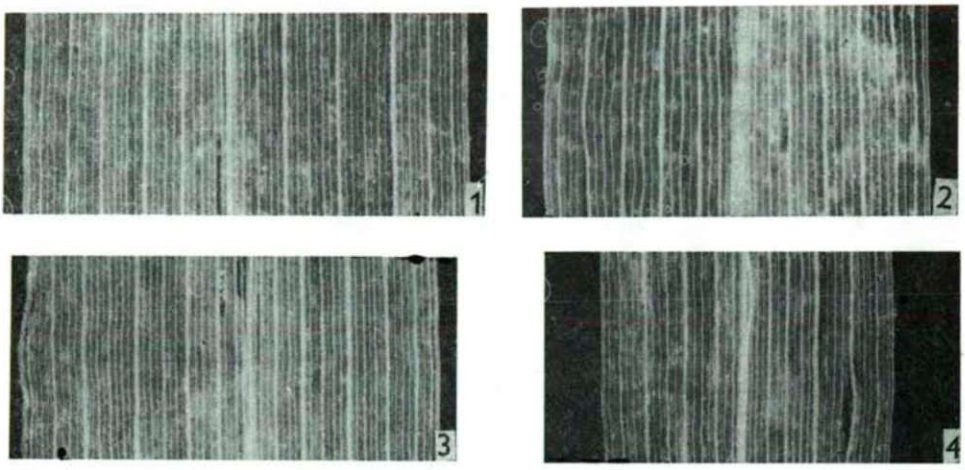


Fig. 2. Arrangement of vein types in the flag (1, 3) and second leaves (2, 4) of GK Szeged (1, 2) and Jubilejnaja 50 (3, 4) in the whole width of the leaves (same magnification).

The area and width of the flag leaves showed strongly negative, while the number of veins per cm showed positive correlation with the net photosynthesis rate (AUSTIN et al., 1982). The value of the bundle length per cm^2 was in agreement with the number of veins/width of leaves in cm (Table 1).

The width of the GK Szeged flag leaves; and the area of the Jubilejnaja 50 cv. flag leaves significantly increased in comparison to the second leaves. Nevertheless, this change was only of small degree compared to the increase in the amount of the veins.

Although the amount of CO_2 uptake under unit of time by the unit of leaf surface showed negative correlation with the width of the flag leaves (AUSTIN et al., 1982); it is probable from the viewpoint of transport of the assimilates that the flag leaves of GK Szeged cv. — which are winder and contain more veins — are more favourable than the narrower leaves of the Jubilejnaja 50 cv.

COMPARISONS BETWEEN THE THICKNESS OF THE FLAG AND SECOND LEAVES

The thickness of the upper two leaves was not identical with the complete width of the lamina. Different values were measured in the case of the variously large veins, and between them, resp., and the thickness showed a decrease towards the edge of the leaves.

It can be seen from the data of Table 2 that in case of both wheats the flag leaves were thicker than the second ones, towards the large lateral (Ll), large intermediate (Li) bundles and the bulliform cells between these. No difference was observed in the thickness of the flag and second leaves of Jubilejnaja 50 cv. in the small intermediate (Si) bundles and the bulliform cells found between them. Significant differences between the two leaves could only be observed at every measuring point in the GK Szeged cv. (Fig. 3, Table 2).

Table 2. Thickness of flag and second leaves in the direction of the Ll, Li, Si bundles and the bulliform cells between them (Llb, Lib, Sib) (See abbreviations in Table 1).

Place of measurings	Leaf thickness (μm) GK Szeged flag leaf		GK Szeged 2 nd leaf	Jubilejnaja 50 flag leaf		Jubilejnaja 50 2 nd leaf
Ll	260.2±5.8	***	238.8±7.5	245.6±0.7	***	220.1±2.4
Llb	209.3±5.2	***	194.7±3.9	189.9±0.8	**	178.8±3.9
Li	218.2±3.6	***	207.0±0.3	197.1±1.6	***	183.2±7.5
Lib	185.6±2.8	***	175.7±0.8	164.5±2.3	NS	163.7±4.7
Si	180.4±5.5	***	173.6±1.2	161.3±5.5	NS	162.9±3.9
Sib	162.9±3.9	***	146.2±4.7	131.9±4.7	NS	133.1±5.9

** : SZD significantion on 1 % level
***: SZD significant on 0.1 % level
NS: no signification

The flag leaves of GK Szeged cv. were expressedly thicker than those of Jubilejnaja 50. It was striking that this was not manifested in the dry weight per unit surface of the flag leaves, since the dry weight of these leaves in GK Szeged was 525 mg dm^{-2}, and the dry weight of Jubilejnaja 50 was 531 mg dm^{-2}. On the contrary, the fresh weight of GK Szeged flag leaves was $2133^{\pm 30}$ mg dm^{-2}, and $2052^{\pm 38}$ mg dm^{-2} in case of Jubilejnaja 50.

The thickness of the flag leaves showed tight correlation with the diameters and areas of the bundles, and the measurements of the mesophyll cells, resp. (LEDENT and POCHET 1978). In the case of the studied two wheats the greater thickness of the flag leaves could firstly originate from the larger size of the veins.

THE MESOPHYLL OF THE FLAG AND SECOND LEAVES

SHAPE AND ARRANGEMENT OF THE MESOPHYLL CELLS

On the transverse section of the wheat leaves and from the perpendicular surface view of the leaves, the mesophil cells under the surface and reverse epidermis were greatly similar to the typical palidase cells (Plate l, Pictures 1, 2, 3,). However, the longitudinal section of the leaves showed that thet mesophyll cells were elongated in a parallel manner with the veins of the leaves and were lobed (TUAN, 1962; CHONAN, 1965; PARKER and FORD, 1982). Therefore, the height and thickness of the mesophyll cells (also corresponding to the lobe diameters) could be measured on the transverse section of the leaves, and the length of the cells, as well as the number of lobes could be recorded from the longitudinal sections (Fig. 1).

The shape, measurements and number of lobes of the arm palisade-like lobed mesophyll cells differed, compared to the cells beside and between the veins. The sclerenchyma edges above and below the larger bundles were bordered by the longest and shortest mesophyll cells having the largest number of lobes. The external thin-walled bundle sheaths were joined by long, many-lobed mesophyll cells, which resembled palisade cells arranged radiately on the transverse sections of the leaves (Plate 1,

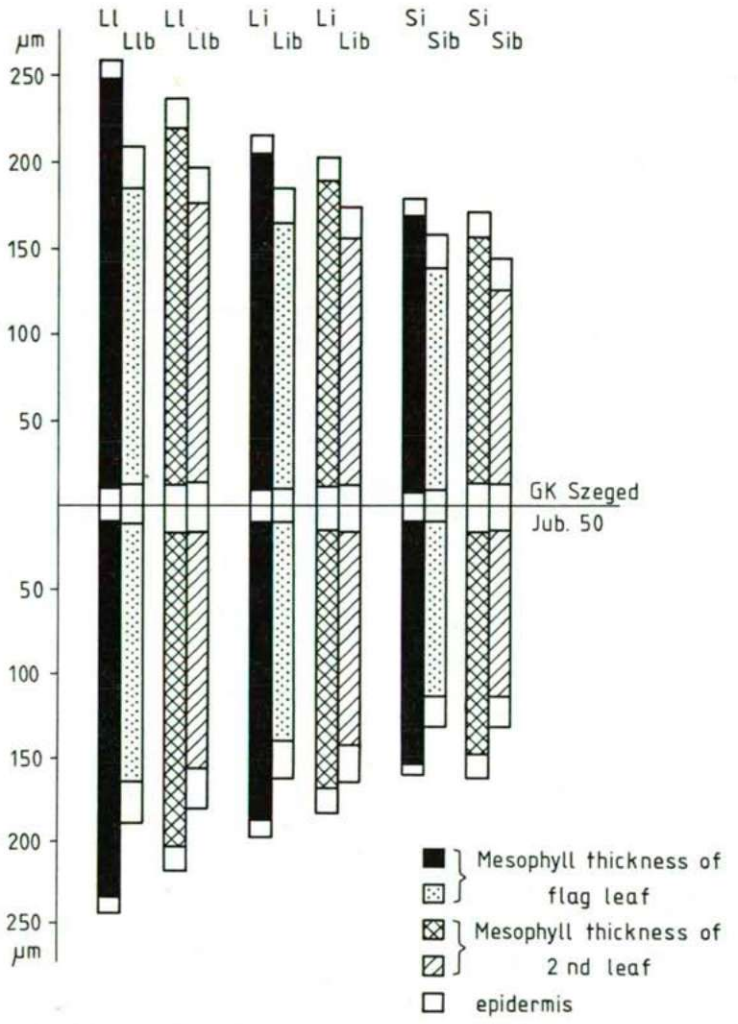
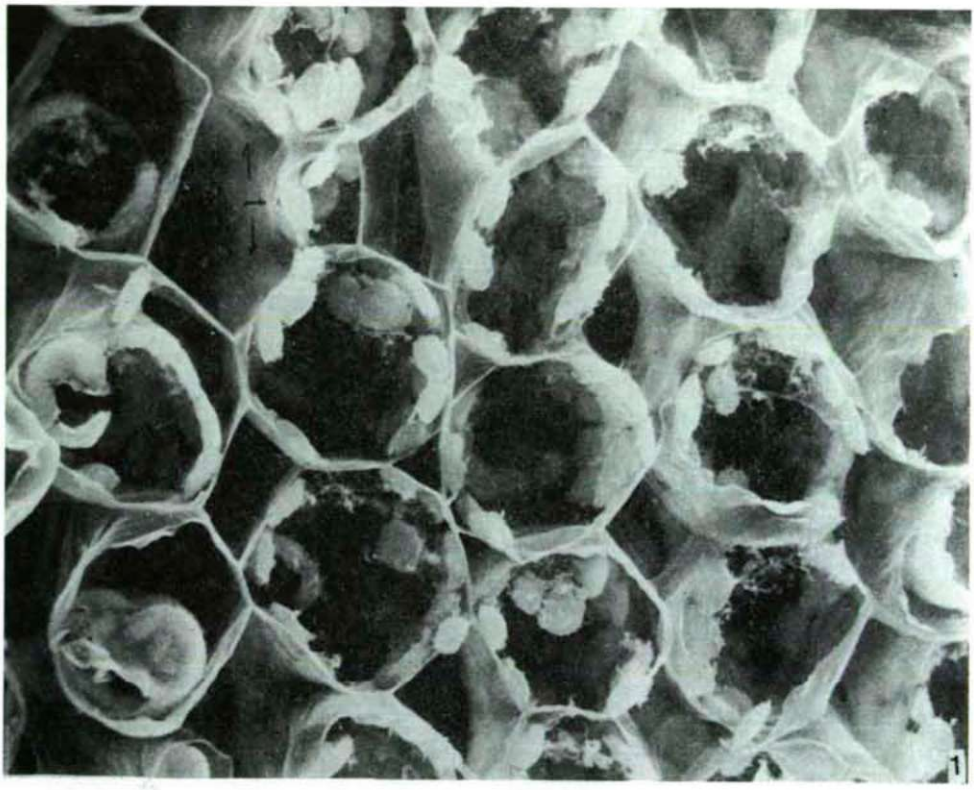
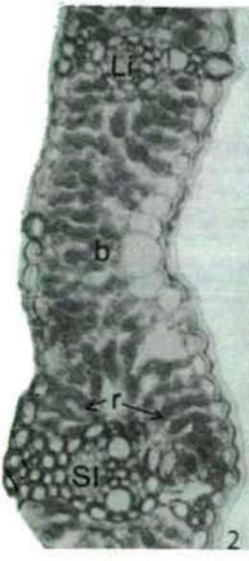


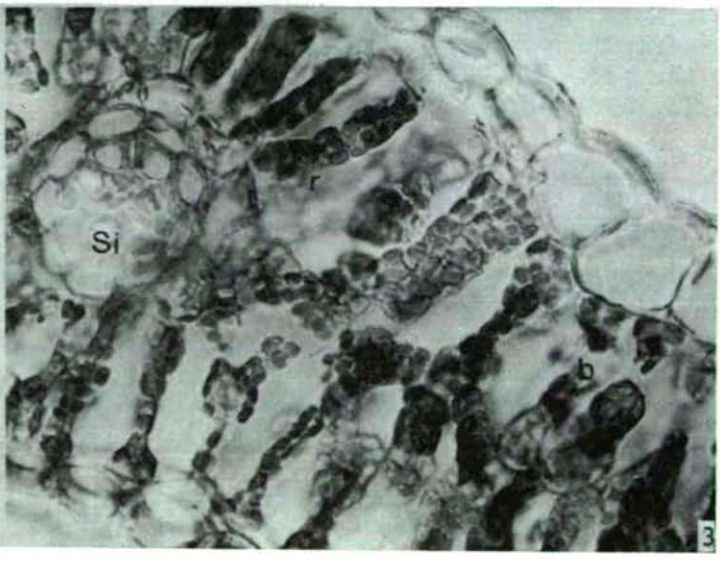
Fig. 3. Changes in thickness of flag and second leawes along the various types of bundles and the bulliform cells between them. (See abbreviations in Table 1).

Pictures 2, 3). The radiately arranged mesophyll cells were in tight junction with each other, the fewest among them were the air-filled intercellular spaces. As it is known, the largest amount of intercellular spaces in the unit volume of the mesophyll can be found under the stoma layers (Plate 1, Picture 2), where characteristically assymetric mesophyll cells with 2—5 lobes can be detected (Fig. 1).

Under the bulliform cells the shorter mesophyll cells having longer lobes, however, showed perpendicular arrangement on the surface of the leaves. The rims of the leaves were lined with sclerenchyma having several cell layers (as are usually the leaves of grass) METCALFE, 1960).




Li
b
r
Si


r
Si
b

MEASUREMENTS OF THE MESOPHYLL CELLS

On the transverse section of the leaves, under the reverse and surface epidermis, resp., the height and width of mesophyll cells were measured beneath the various sized bundles and bulliform cells found among them (Table 3, Fig. 1). It could be seen from the results of the measurings that the mesophyll cells between the veins the flag second leaves were essentially higher and wider (thicker) than those beside the veins.

Compared to the second leaves the height of the mesophyll cells was lower, and the width (lobe diameters) wider under the bulliform cells in the flag leaves of the Jubilejnaja 50 cv. On the contrary, in the flag leaves of GK Szeged cv. the mesophyll cells between the veins showed only slight changes in height and the width was found to be decreased in comparison to the second leaves.

In the height of the mesophyll cells (Table 3) it could not be manifested unambiguously that the flag leaves were thicker than the second leaves (Fig. 3). The greater

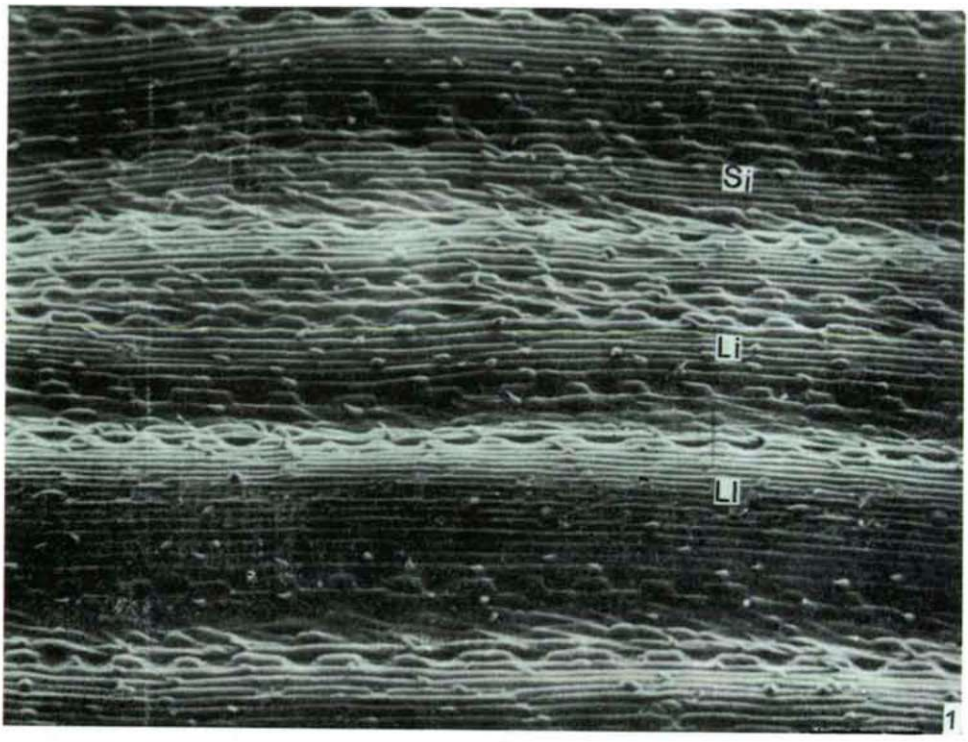
Table 3 Measurements of mesophyll cells in flag and second leaves

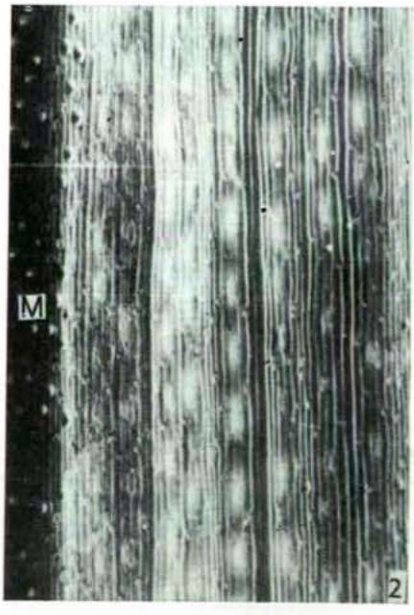
		Flag leaf		2 nd leaf	
		Adaxial position	Abaxial position	Adaxial position	Abaxial position
GK Szeged					
Ll		25.5±4.5*	26.6±4.6	28.3±3.6	28.1±3.8
Li	cell height	26.6±3.4	24.3±3.7	26.4±3.6	26.4±3.8
Si	cell height	29.4±2.6	24.6±3.4*	27.2±4.8	27.0±7.0
Bc		45.0±3.0	39.2±4.8	44.2±5.8	41.9±5.9
Ll		10.6±3.4	10.6±1.4*	10.4±1.5	11.9±2.0
Li	cell thickness	9.6±2.4	9.6±2.4	10.2±3.7	10.5±4.8
Si	cell thickness	9.8±2.2	9.0±3.0*	9.2±2.7	10.5±1.5
Bc		11.4±2.6*	12.2±1.8	14.4±3.6	13.3±2.7
Jubilejnaja 50					
Ll		27.7±4.3*	27.4±4.6	24.3±1.7	25.6±4.4
Li	cell height	25.0±3.0	26.9±3.1	26.2±3.8	27.8±2.2
Si	cell height	29.1±5.1	26.5±3.5*	29.6±2.4	29.5±3.5
Bc		33.8±6.2*	31.4±7.4*	44.6±3.4	37.2±5.8
Ll		10.9±1.1	10.4±1.6	11.0±3.0	10.6±1.4
Li	cell thickness	9.8±2.2	10.7±1.3*	10.2±1.8	9.4±2.6
Si	cell thickness	10.6±1.4	10.0±2.0*	10.6±1.4	8.8±1.2
Bc		14.1±3.9*	12.6±3.4*	12.2±1.8	9.5±1.5

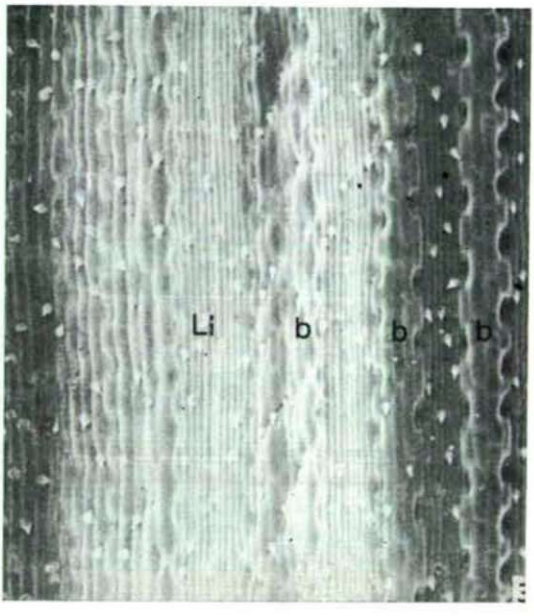
Measurements were made on the transverse section of the leaves from the midrib to the leaf margin: in the direction of the large lateral (Ll), large intermediate (Li), small intermediate (Si) bundles and the bulliform cells (Bc) between them, under the reverse and surface epidermis of the mesophyll cells. The height and thickness of the cell were measured. (The cell thickness or width is equivalent to the lobe diameter).

*: The value measured in the flag and second leaves is significant on 5% level.

Plate I. Form of mesophyll cells: Picture 1: SEM picture of the lobes of mesophyll cells filled with chloroplasts (1), with the surrounded intercellulars, from a view perpendicular to the abaxial surface. (GK Szeged flag leaf, M: ~1250 x). Pictures 2.3: Light microscopic picture of transverse section of Jubilejnaja 50 flag (Picture 3, M: 640 x) and second leaf (Picture 2, M: 200 x) with small lateral (Sl), large intermediate (Li) and small intermediate (Si) bundles, mesophyll cells under the radial (r) and bulliform (b) cells.


Si
Li
Li
1


M
2


Li
b
b
b

thickness of the GK Szeged and Jubilejnaja 50 cv flag leaves firstly originated from the larger size of the large lateral and large intermediate bundles.

In the case both studied corn types the height of the mesophyll cells on the abaxial side of the flag leaves, under the small intermediate bundles and between the veins (Table 3) showed a decrease compared to the second leaves. The determination of LEDENT and POCHET (1978) that the thickness of the flag leaves showed positive correlation with the measurements of the mesophyll cells is not considered by us to be exact, and our measurings did not support this. The height of the mesophyll cells showed a decrease, and the length an increase on the effect of weak light intensity (FRIEND and POMEROY, 1970).

The light conditions of the flag leaves were not worse than those of the second leaves, nevertheless the centre parts of the leaves were rather of a horizontal position and therefore the abaxial side may be more shadowed than that of the second leaves, which slope better. On the abaxial side of the Jubilejnaja 50 cv flag leaves the height of the mesophyll cells under the bulliform cells also showed a more significant decrease in comparison to the second leaves (Table 3), and this result cannot be explained by the changes in light intensity.

THE NUMBER OF LOBES PER CELL

The percental distribution of the frequency of the number of lobes per cell was studied in two ways on the longitudinal sections of the leaves. On the one hand the lobes of 200 randomly-selected mesophyll cells were counted on the longitudinal sections (Fig. 4, first A column row). In the other „casual samples" only the lobes of the mesophyll cells beneath the bulliform cells (cc. 40 cells were counted (Fig. 4, second B column row).

It was a uniform characteristic in the case of both wheat types that the multilobed mesophyll cells were more frequent in the flag leaves than in the second leaves (Fig. 4). For example, in the GK Szeged cv. flag leaves the 8-lobed mesophyll cells situated under the bulliform cells occurred with a frequency of 45 %, and 13 % in the case of the second leaves. This difference in the number of lobes was more intensive in the Jubilejnaja 50 cv. flag and second leaves (Fig. 4).

The question is: what anatomical characteristics is the increase in the number of lobes per cell of the flag leaves connected with?

It is known that in the upper leaves of wheat the mesophyll cells are larger and have more lobes than in the lower leaves (CHONAN, 1965). According to our opinion the mesophyll cells of flag leaves are not in general larger, but rather longer than those of the second leaves. The mesophyll cells of the flag leaves of the hexaploid *T. Aestivum* cv. Professeur MARCHAL are twice as high and double-lobed than those of the diploid T. urartu (PARKER and FORD, 1982). On the effect of the decrease in light intensity both the length and number of lobes of the mesophyll cells increased (FRIEND and POMEROV, 1970).

According to our studies one of the main causes of the increase in lobe-number of the flag leaves (compared to the second leaves) may be the greater elongation of the mesophyll cells and the decrease in the height of the cells. In the flag leaves, the

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Plate II. SEM picture of the arrangement of the cell types forming the ad- and abaxial epidermis of the flag leaves: GK Szeged adaxial (Picture 1) and abaxial (Picture 2) area; Jubilejnaja 50 adaxial (Picture 3) area (M: ~50 x).
Ll = large lateral, Li = large intermediate; Si = small intermediate bundles, b = bulliform cells, M = midrib,

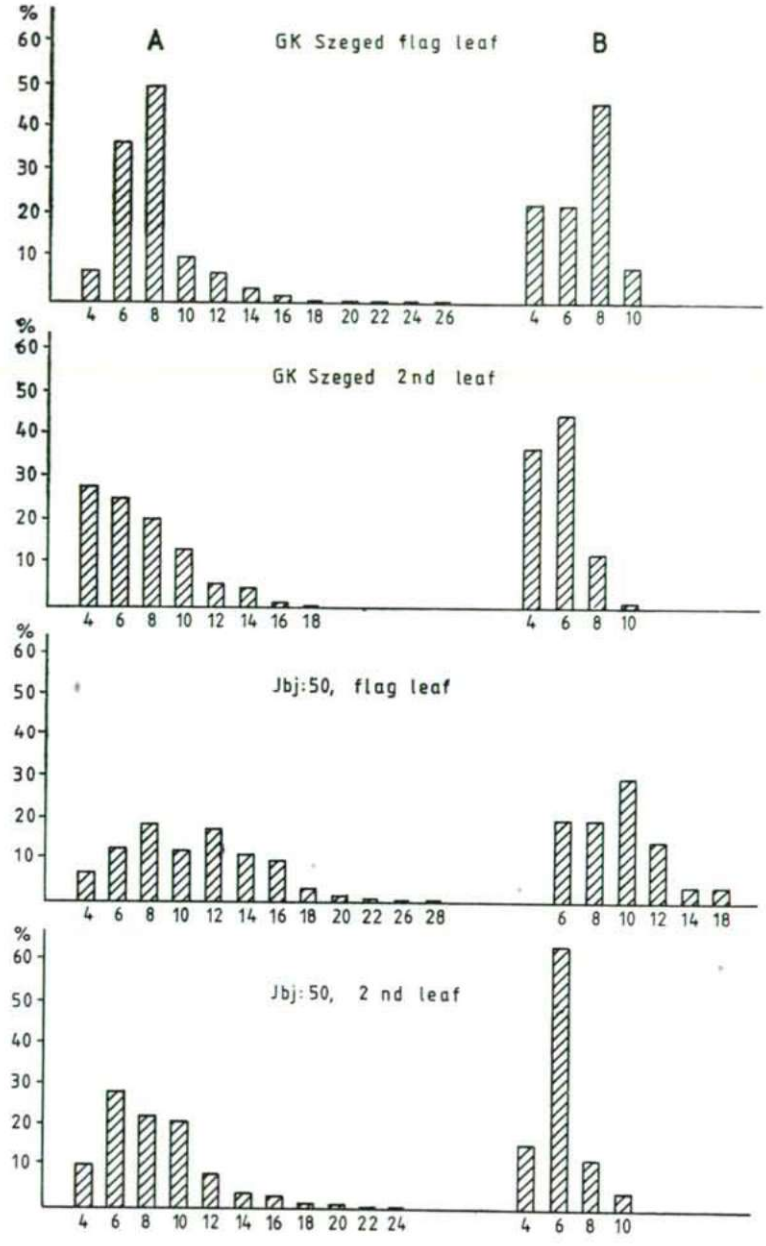


Fig. 4. Percental distribution of the lobe number of mesophyll cells in the flag and second leaves of GK Szeged and Jubilejnaja 50. Casual distribution (randomly selected sampling) from the mesophyll of the whole leaf (A) and only from the part of the leaf under the bulliform cells (B).

other cause of the higher incidence of many-lobed mesophyll cells is with all probability that the veins of these leaves (number of veins per cm of leaf width) show significantly greater density than in the second leaves. Therefore, the long, many-lobed

mesophyll cells situated radiately along the veins can be found in higher, while the shorter ones with fewer lobes situated between the veins can be observed in smaller percentage in the mesophyll in the case of flag leaves than in that of the second leaves.

Definite difference could be detected betwween the two wheat types concerning the percental distribution of the lobe numbers per cells. The many-lobed mesophyll cells were more frequent in both leaves of the Jubilejnaja 50 cv. than in the leaves of the GK Szeged cv. For example, beneath the bulliform cells the mesophyll cells having ten or more lobes were found to occur with a frequency of 58% in the Jubilejnaja 50 cv. flag leaves, and with a freqeancy of 7% in the GK Szeged cv. flag leaves.

COMPARISON BETWEEN THE ADAXIAL AND ABAXIAL SURFACE OF THE FLAG LEAVES

The two surfaces basically differed from each other in cell types, measurements, arrangement, stoma- and trichome amount, density of silica cells and epicuticular wax needles (Table 4).

Table 4. Changes of measurement stoma— and trichome number in guard cells

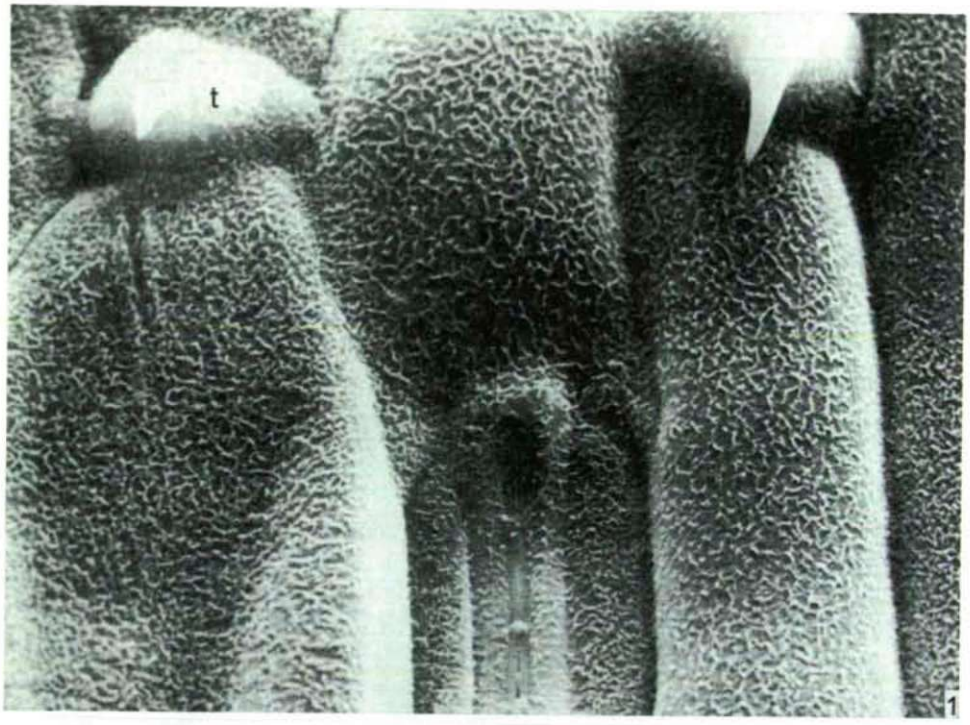
	GK Szeged, Flag leaf			Jubilejnaja 50, Flag leaf		
	Adaxial position		Abaxial position	Adaxial position		Abaxial position
In conditioned climate room						
stoma guard cell length μm	60	***	55	60		61
stoma number/cm^2	4696	***	4102	4075	***	3016
trichome number/cm^2	3440		1452	3482		1581
In the fields						
stoma guard cell length μm	60	***	55	60	***	55
stoma number/cm^2	6289	***	4809	5141	***	3756

*** = SZD significant on 0.1% level.

The nature of the adaxial surface was determined by two cell types: the epidermis cells of the costal field covering the veins, protruding above the large veins; and those of the intercostal field, resp., as well as the sections of bulliform cells (Plate 1, Picture 2; Plate 2, Picture 1; Plates III. IV, Picture 2).

Narrower epidermis cells were found to extend over the sclerenchyma cells connected with the larger veins, than over the smaller veins mesophyll cells between the veins. The stoma — between the eveins — were also arranged in longitudinal rows. The bulliform and sclerenchyma-covering epidermis cell rows were also free of stoma (Plate II, Pictures 1, 3). The larger veins were protruded on the adaxial surface, due to which the surface was slightly undulatory (Plate I, Picture 2; Plate II, Pictures 1, 3). Silica cells and needle-sharp trichomes leaning to the side were sporadically found among the epidermis cells (Fig. 5., Plate II, Picture 1., Plates III, IV., Pictures 1, 2). Longitudinal cuticule striation and compactly situated epicuticular wax needles were observable on the cell surfaces (Plate IV., Picture 2, Fig. 5).

The abaxial surface was characterized by the alternation of sections made up of epidermis cells, narrower and longer above the larger veins, and wider above the mesophyll cells (Plate II, Picture 2, Plate V. Picture 3). The various types of veins had



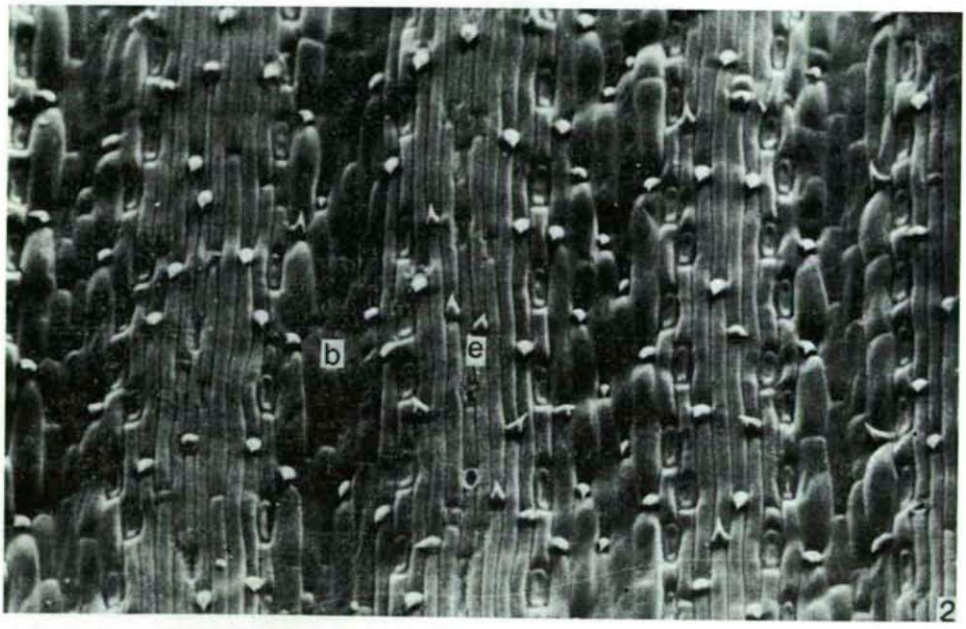


Plate III. SEM picture of sections formed by epicuticular wax needles (Picture 1, M: ~1050 x) and bulliform (b), as well as epidermis cells (e) (Picture 2, M: ~100 x). t = trichome.

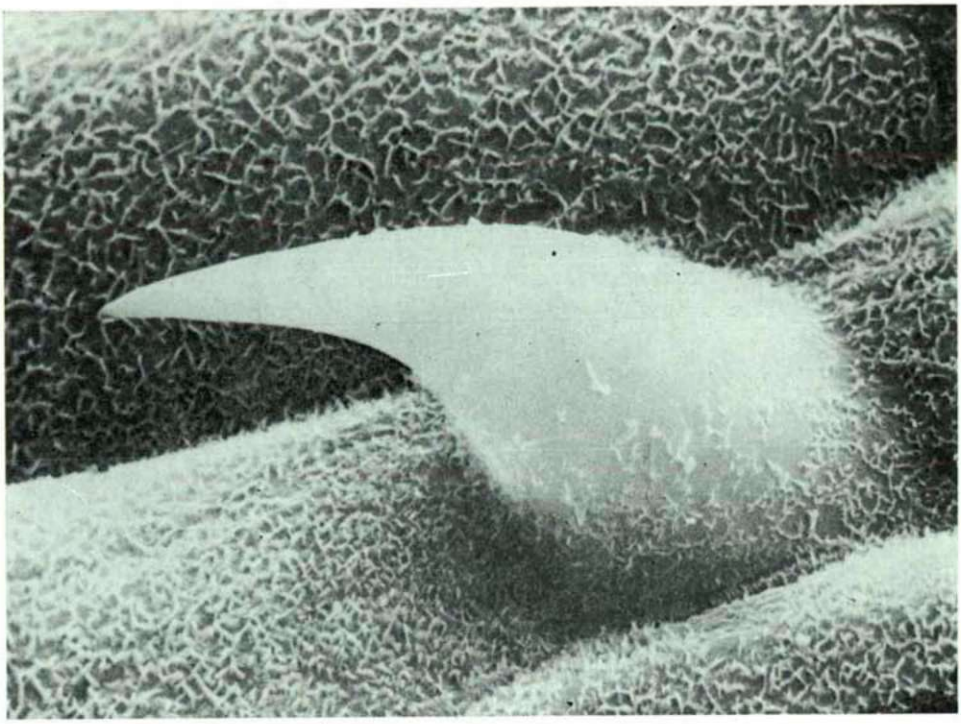


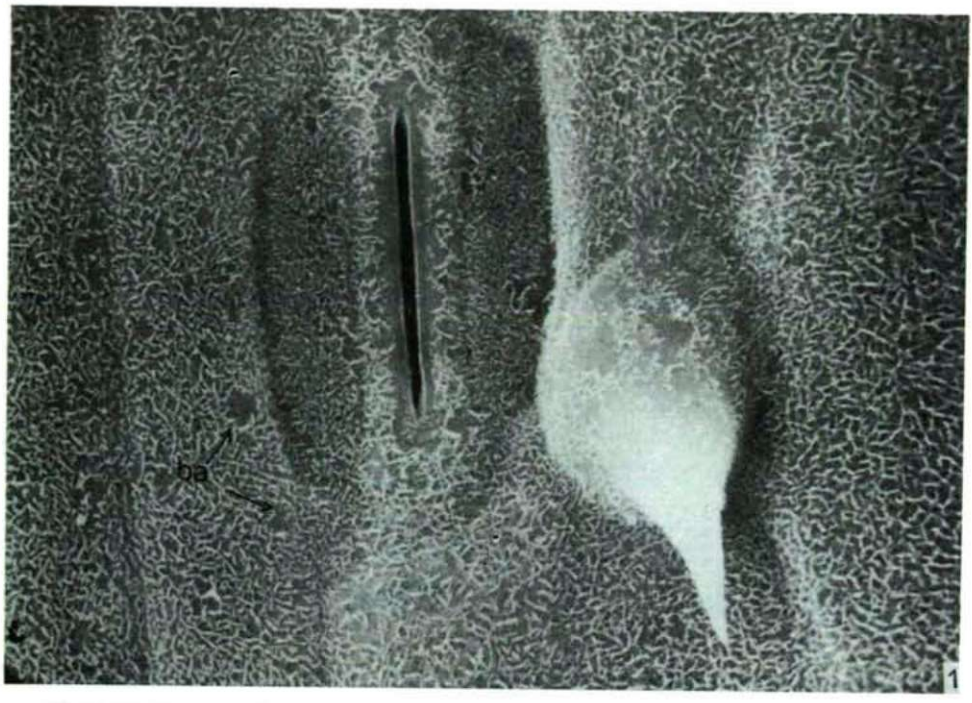
Fig. 5. Adaxial surface in GK Szeged cv. — wax needles, unicellular trichomes. M = ~ 2500 x.

determinant role, as is generally characteristic of the epidermis of grass (METCALFE, 1960; ESAU, 1969; WOLCSÁNSZKY, 1972). The main vein was strongly protruded, the larger veins only slightly; thus this surface was almost even compared to the adaxial side (Plate 1, Picture 2 Plate II, Picture 2).

The trichomes of the abaxial surface were bluntly conoid, observable above the larger veins. The main vein was the most densely covered by them. The greater density of the silica cells (Plate II, Picture 2, Plate V. Picture 2. 3) and the scarce epicuticular wax-covering (Plate V, Picture 1) were characteristic features. The epidermis above the sclerenchyma (costal field) was stoma-free, which was well observable on polarization electron-microscopic pictures (Plate V, Picture 2). On both surfaces the stomata were slightly subsided.

Great differences in stoma number were detected regarding both types between the plants grown in the fields and climate room. The stoma number of the plants grown in the fields was essentially higher, e.g. by more than 25% on the adaxial surface.

On SzD level a difference of 0.1% was observed in stoma number between the two surfaces, also, on the basis of the results related both to the climate room and the fields. In the case of both wheats the stoma number on the abxaial surface was lower: 86% (climate room) and 76% (fields), resp. of the amount detectable on the adaxial surface in GK Szeged; and 75% (climate room) and 73% (fields) in the case of Jubilejnaja 50.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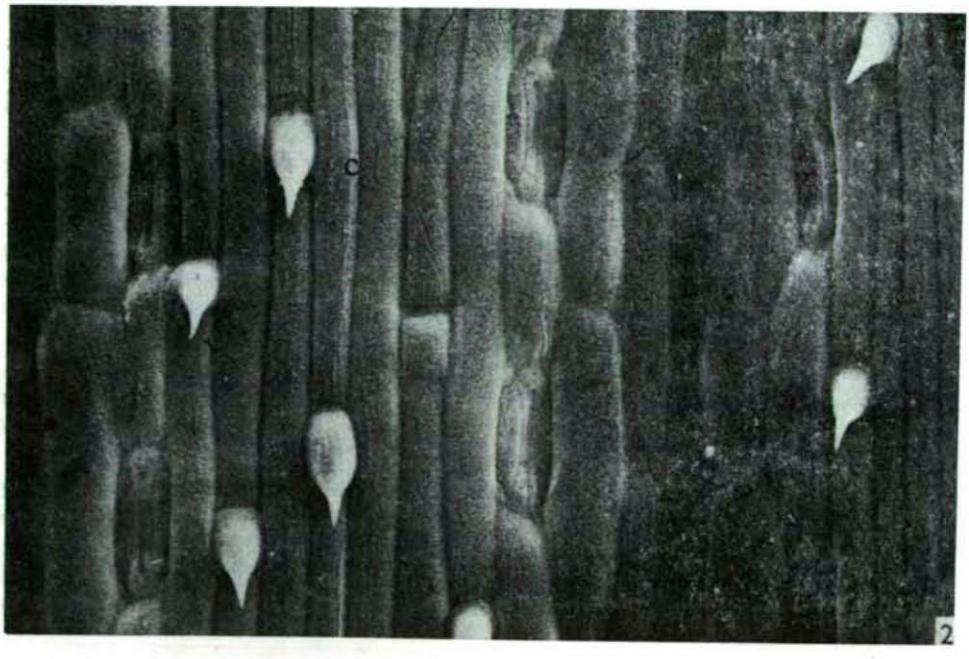
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AUSTIN et al. (1981) also obtained higher stoma number in mean values on the adaxial surfaces related to 15 wheat genotypes.

The frequency of stomata is always higher on the leaf surfaces than on the reverse sides in the *Triticum* species and types (TEARE et al., 1971) There are also significant differences between the two types on the basis of the stoma number on both surfaces. The stoma number of the GK Szeged cv. flag leaves is higher on both surfaces (Table 4).

On the flag leaves on the *Triticum* and *Aegilops* species the stoma incidence is in positive correlation with the maximal rate of photosynthesis (AUSTIN et al..1982). It is also expectable on the basis of the higher stoma amount of GK Szeged that the flag leaves bind more carbon dioxide related to unit surface, than the flag leaves Jubilejnaja 50 cv. The difference between the two surfaces is greater in trichome number. The amount of trichomes on the abaxial surface was only 42% (GK Szeged — climate room) and 45% (Jubilejnaja 50 — climate room), resp. of that on the adaxial surface (Table 4).

The measurements of the guard cells were compared on the basis of the length of two guard cells; as their joint width largely depends on the degree of openness of the stoma. On the adaxial side of the GK Szeged cv. flag leaves the average length of the guard cells was also greater besides greater stoma density (Table 4).

Great difference could be observed between the two surfaces in the amount of epicuticular wax. The adaxial surface of the flag leaves of both wheats was compactly covered by wax needles — except the protruding parts of the trichomes and the cuticle helix around the stoma (Plates III, IV., Picture 1). The density of the wax rods was greater on the adaxial surface of GK Szeged cv., than Jubilejnaja 50 cv. On the contrary, the wax needles were scarcely observed on the abaxial surface Plate V, Picture 1). The wax covering was not even on the adaxial surface, expressedly in the Jubilejnaja 50 cv. smaller-larger bare areas were detectable on this surface (Plates III, IV. Picture 1).

On the basis of the ratio of the surface wax coating and bare areas — in their studies on maize leaves — GÖRÖG et al. (1981) consider it to have determinant role in the permeation of herbicides and other substances through the surface.

STRUCTURE OF MESOPHYLL AND PHOTOSYNTHESIS

Since it has been proved that at high light intensity the flag leaves of diploid wheats have higher net photosynthesis rate than those of hexaploids (KHAN and TSUNODA, 1970; EVANS and DUNSTONA, 1970; GIFFORD and EVANS, 1973, AUSTIN et al., 1982), sereval authors interprent this also with the anatomical structure of the leaves (DUNSTONE and EVANS, 1974; PARKER and FORD, 1982; AUSTIN et al., 1982).

Those data (BONSTRA, 1937; SIMPSON, 1968; FOCKE, 1973; NALBORCZYK, 1978) according to which the flag leaves have significant role compared to other leaves in the formation of assimilates stored in the grains also raise the conception that there is a difference in the tissue structure of the flag and second leaves, too.

CHONAN (1965) demonstrated that the mesophyll cells of the upper leaves of wheat rea larger and more lobed than the lower ones. With the increase in lobe number the ratio

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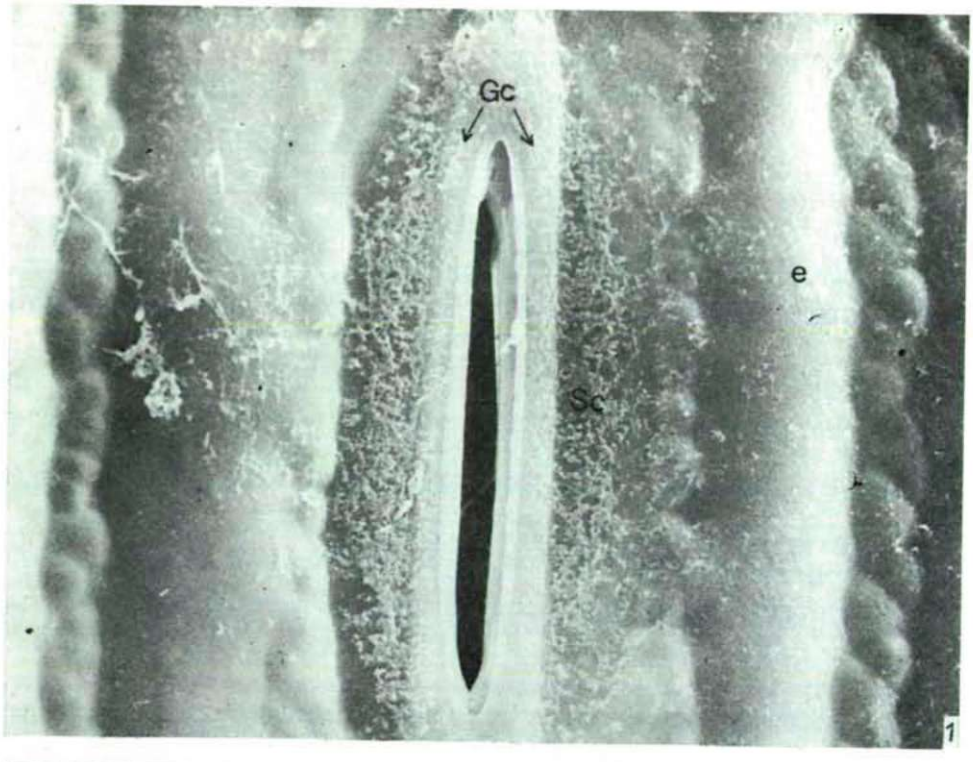
Plate IV. Adaxial surface of Jubilejnaja 50 flag leaf: Picture 1: Smaller-larger "bare areas" (ba) between the epicuticular wax needles (SEM, M: ~1250 x). Picture 2: Longitudinally running cuticle stripes (above the vein) (C) and the "bare areas" on the outer tangential wall of the epidermis cells. (M: ~300 x).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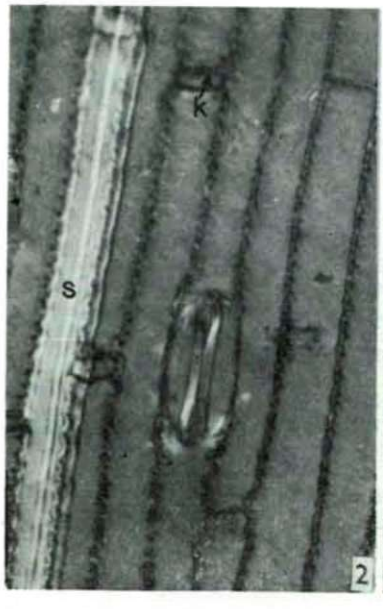
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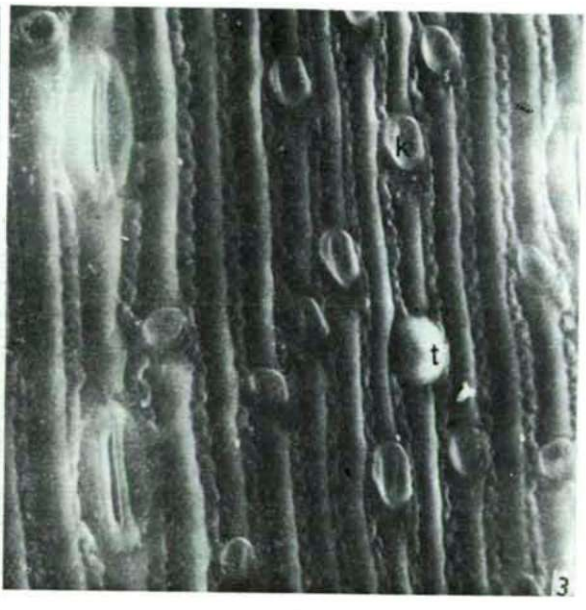
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of cell area per cell volume also increases, and this — according to our assumption-makes possible a more intensive gas exchange (binding of carbon dioxide).

The length and number of lobes of the mesophyll cells of the hexaploid *T. aestivum* cv. Professeur Marchal flag leaves are the double that of the diploid T urartu cells, but in contrast to the publication of CHONAN (1965) the cell area per cell volume ratio does not differ singificantly (PARKER and FORD, 1982). At the same time the net photosynthetic rate referring to the unit leaf area of the Professeur Marchal is 26 mg CO_2 $dm^{-2}h^{-1}$; being significantly lower than that of *T. urartu,* which is 43 mg CO_2 $dm^{-2}h^{-1}$ (AUSTIN et al., 1982).

From the point of view of CO_2 uptake PARKER and FORD (1982) consider rather the area of the air-filled intercellular space, and the ratio of internal exposed mesophyll cell area to external leaf area, resp. to be important; and not the whole mesophyll cell area. If this ratio increases, there is a decrease in the resistance in the diffusion of carbon dioxide into the mesophyll cells.

The intercellular surface per leaf area ratio is 15.3 in case of *T. urartu;* this is higher thau iu case of Professeur Marchal, where it is 10.5 (PARKER and FORD, 1982). Therefore, it is not in contrast with the variation of net photosynthesis in these two wheat types; according to our epinion, however, this explanation is not satisfactory.

Apart from the above, PARKER and FORD (1982) also bring the higher photosynthetic rate of *T. urartu* in connection with the fact that in the flag leaves of *T. urartu* the watetmovement of the photosynthates and between the veins and chloroplasts is possibly longer — due to the more dense situation of the veins — than in the case of P. Marchal, where there is a greater distance between the veins.

The afore-described notions are supported by experiments, nevertheless, in our opinion they are one-sided and there is still no satisfactory exlpanation to the integrated functioning of the mesophyll; the significance of the lobed structure of mesophyll cells; the cause of the changes in lobe number.

According to our assumption the lobed structure of the mesophyll cells has two essential significances: First, the cell volume is capable of increasing in such „quantum" manner (hexaploid wheats), that the cell area only decreases in a small degree, resp., the cell area per cell volume ratio does not change essentially. Second, the lobed structure makes possible a more effective adaptation to the differing light conditions. When the mesophyll cells under the epidermis become elongated, they become many-lobed and their height decreases (Table 3, Fig. 4). Thus, in one cell, close to the surface (light) there are several such chloroplasts which throw less shadow on each other and accommodate better to the high light intensity. In the mesophyll of flag leaves the ratio of longer and many-lobed mesophyll cells increases; that of the high and shorter cells decreases with the increase in density of the veins (related to the second leaves) (Fig. 4).

It has been demonstrated in our earlier publications (MARÓTI, 1976; MARÓTI and GÁBOR, 1976) that in the palisade chloroplasts, the amounts of chlorophyll-b, neoxanthine, and lutein characteristic of the II. photochemical system are lower, and the area of adhered membranes (grana thylakoids) is smaller than in the spongy parenchymal

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Plate V. Picture 1: Scarce wax-coating on the abaxial surface of GK Szeged flag leaf (SEM, M: ~ 1250 x) Gc = guard cell, Sc = subsidiary cell, e = epidermis cell. Picture 2: Polarization light microscopic picture of the narrow epidermis cells of the abaxial surface, above the stoma-free sclerenchyma (s). GK Szeged second leaf, M: 300 x) K = silica cell. Picture 3: SEM picture of the sections of stoma-lined, wide epidermis cells and those densely covered by stoma-free trichomes (t), silica cells (K). (M: ~300 x).

chloroplasts. It is also known from the study of SKENE (1974) that the individual lamella (granum ratio increases significantly in the palisade cell chloroplasts. Furthermore, the „palisade character" increases in the flag leaves.

On the basis of the above, it is assumed that in the chloroplasts of wheat flag leaves also (compared to the second leaves), there is a higher ratio of stoma lamellae, and cyclic photophosphorylation providable to this membrane, resp. (and relatively independent of the linear electron transport). In case of high light intensity therefore, the chloroplasts of flag leaves produce more ATP than those of the lower leaves, and this enables enhanced triosphosphate transport from the chloroplasts, and saccharose transport from the cytoplasm.

It the above hypothesis is applied to the two wheat types, the result is that Jubilejnaja 50 cv is a species accommodating better to high light intensity; but its net photosynthetic rate may be lower; its cyclic photophosphorylation more ample than in case of GK Szeged cv.

Nevertheless, further and many-sided experiments are necessary to become familiar with the facts.

Acknowledgement

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