STUDIES ON THE PHOTOSYNTHETIC TISSUES IN THE LEAVES OF CEREAL CROPS I. THE MESOPHYLL STRUCTURE OF WHEAT LEAVES AT DIFFERENT LEVELS OF THE SHOOT

著者	CHONAN Nobuo
journal or publication title	Tohoku journal of agricultural research
volume	16
number	1
page range	1-12
year	1965-10-25
URL	http://hdl.handle.net/10097/29459

STUDIES ON THE PHOTOSYNTHETIC TISSUES IN THE LEAVES OF CEREAL CROPS I. THE MESOPHYLL STRUCTURE OF WHEAT LEAVES AT DIFFERENT LEVELS OF THE SHOOT

By

Nobuo CHONAN

Department of Agronomy, Faculty of Agriculture, Tohoku University, Sendai, Japan
(Received March 15, 1965)

Introduction

In many plants, the mesophyll is commonly differentiated into palisade and spongy parenchyma, and is specialized as a photosynthetic tissue. The cells of the palisade parenchyma are usually elongated in shape, and are regularly oriented with their long axes at right angles to the leaf surface. The spongy parenchyma appears less regular and has conspicuous intercellular spaces. In general the mesophyll of grasses, however, shows no distinct differentiation into palisade and spongy parenchyma. The arm-plaisade cells from which several lateral protuberances or arm-like branches developed are found in some grass leaves (3, 4, 5).

The mesophyll structure of cereal crops have not been observed in detail. In this study the mesophyll structure of leaves inserted at different levels of the shoot of wheat plant were observed.

Materials and Method

Germinated seeds of winter wheat, variety Aobakomugi, were sown in 1/5000 a Wagner pots on October 18 1962. The plants were grown outdoors and received normal soil cultural treatment, but received no manures. At the 2-leaf stage, the seedlings were thinned and five plants were left per pot. At the begin-ing of active growth in the early spring, two plants were left per pot through the second thinning. As soon as each successive leaf blade ceased elongation, it was preserved in FAA. In the middle portion of the 5th, 11th and 13th (uppermost) leaf blades, serial sections were cut by the parafin method in transverse (15μ or 25μ in thickness) and longitudinal (10μ to 12μ in thickness) planes. The sections were stained with safranin and Delafield's hematoxylin. In the 5th, 8th, 11th and 13th leaves, the abaxial surface of the mesophyll were microscopically observed.

Result

In the case of wheat leaves, most of the mesophyll cells are the so-called arm-palsiade cells. These cells are seen as a complicated cell which possess several lateral protuberances developed at right angles to the leaf surface. The number of protuberances are approximately the same on both sides of a cell. This structure is not seen in the transverse sections (Plate 1-A, 2-A), but clearly seen in the longitudinal sections (Plate 1-B, C, 2-B, C).

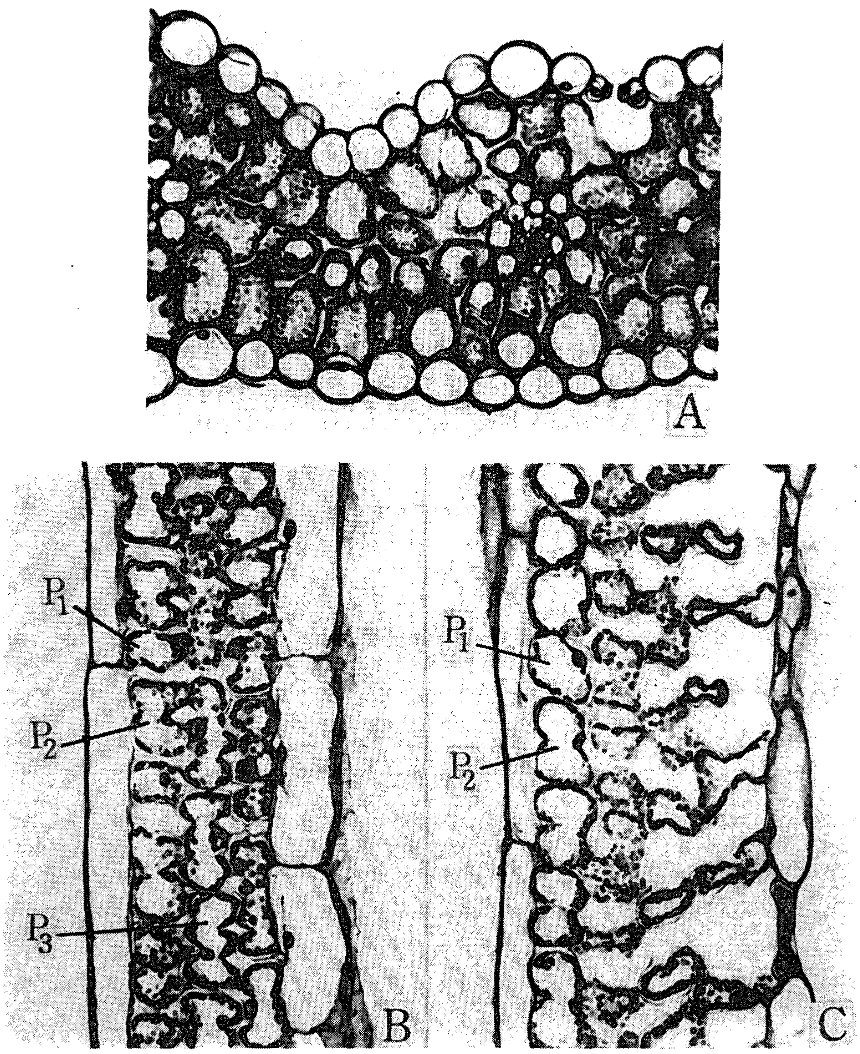

Plate 1. Mesophyll structure of the 5th leaf.

A, transection. B, longitudinal section cut at the middle portion between the vascular bundles. C, longitudinal section cut at the row with stomata. The arm-palisade cells of P_1-P_3 are seen in the longitudinal sections. (A11, × 180.)

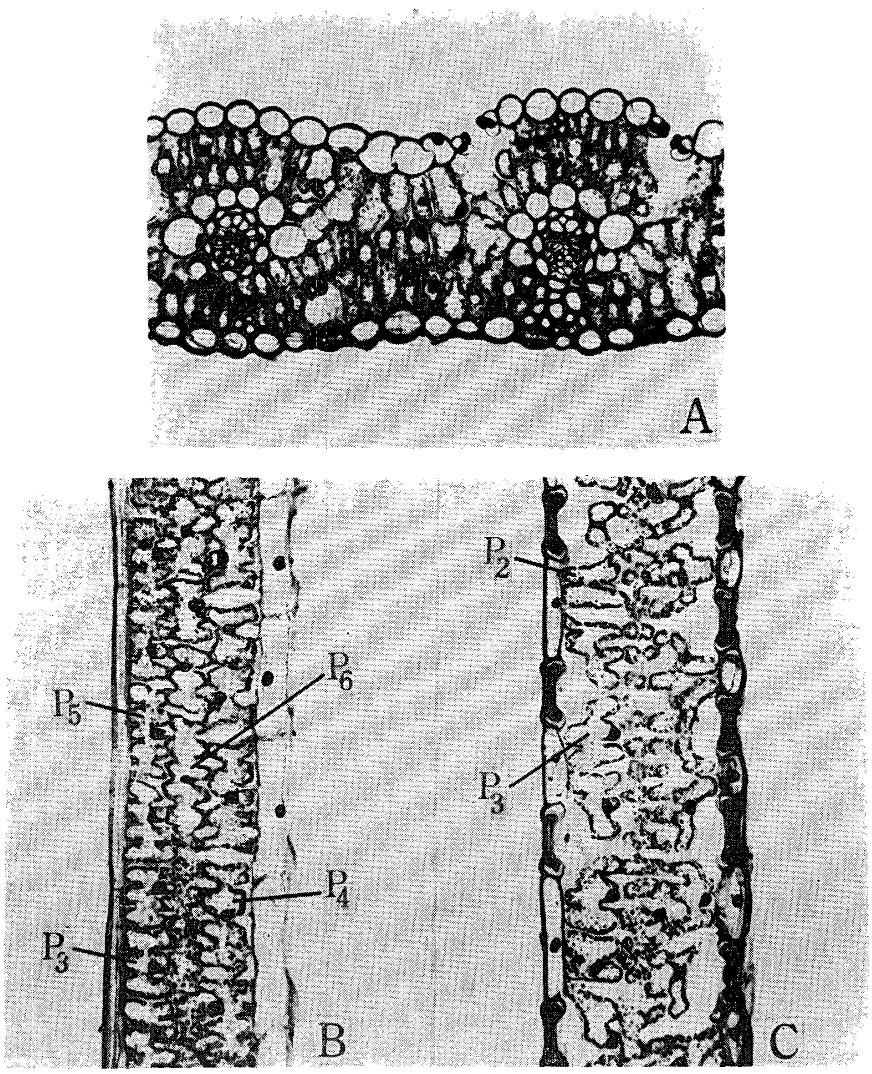

Plate 2. Mesophyll structure of the 13th (uppermost) leaf.

A, transection. B, longitudinal section cut at the middle portion between the vascular bundles. C, longitudinal section cut at the row with stomata. The arm-palisade cells of P_2-P_6 are seen in the longitudinal sections. (A11, ×180.)

Model of the arm-palisade cell is shown in Fig. 1. Fig. 1-a is a diagram of longitudinal section, cut at right angles to the leaf surface, and Fig. 1-b is a transverse section. When the mesophyll cells are observed from the leaf surface, the protuberances are seen in circles (Fig. 1-C, Plate 3). The protuberance diameter (r) is nearly the same as the cell thickness (T).

The number of protuberances, developed on the one side of a cell, are from two to twelve. These cells are expressed as P_2, P_3, ... P_{12} respectively, according to the number of protuberances. The most simple shape of the cell, expressed as P_1, is slightly elongated without developing protuberance (Plate 1–B,

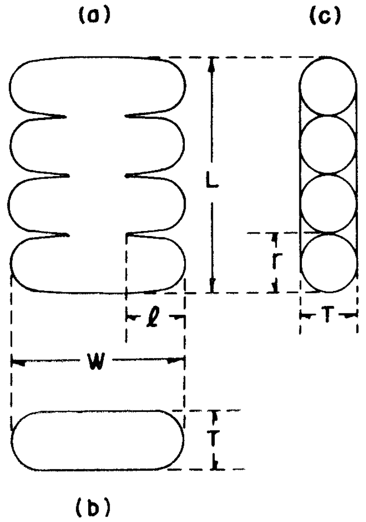

Fig. 1. Model of the arm-palisade cell.
L: cell length l: protuberance length
T: cell thickness r: protuberance diameter
W: cell width

C, 2–B, C).

Distribution of these cells in relative rate are shown in Fig. 2. Figure shows that the number of protuberances and the distribution increase from the lower to the upper leaves. The distribution depends on the portion of the leaf balde. The mesophyll cells near the vascular bundles have more protuberances in number than the cells between the vascular bundles. The cells in the middle layer have more protuberances in number than those in the abaxial and adaxial layers. In the area adjacent to the stomata the development of protuberances or the enlargement of cells are depressed, and there are conspicuous intercellular spaces (Plate 1–C, 2–C).

As shown in Fig. 3, the cell length (L) varies in the range of $30\sim150\mu$, and there are positive linear relationships between the number of protuberances and the cell length as far as the leaves in the same level are concerned. The slope of lines fall in the upper leaves, i.e. the cells in the upper leaves have more protuberances in number than the cells of the same length in the lower leaves. The average cell length calculated from the data of Fig. 2 and Fig. 3 is 52μ in the 5th leaves, 70μ in the 11th and 13th leaves respectively.

The protuberance diameter (r) calculated from the data of Fig. 3 is shown in Fig. 4. They are remarkably decreased from P_1 to P_3, as the number of protuberances increase, and the upper leaves have smaller diameter protuberance than the lower leaves. From the result of Fig. 2 and Fig. 4, it is clear that the diameter of protuberance near the vascular bundles is smaller than that of the other portions. These results are also shown in Plate 3, photographed from the abaxial surface, in which a circular unit indicates a protuberance and one cell is composed of these

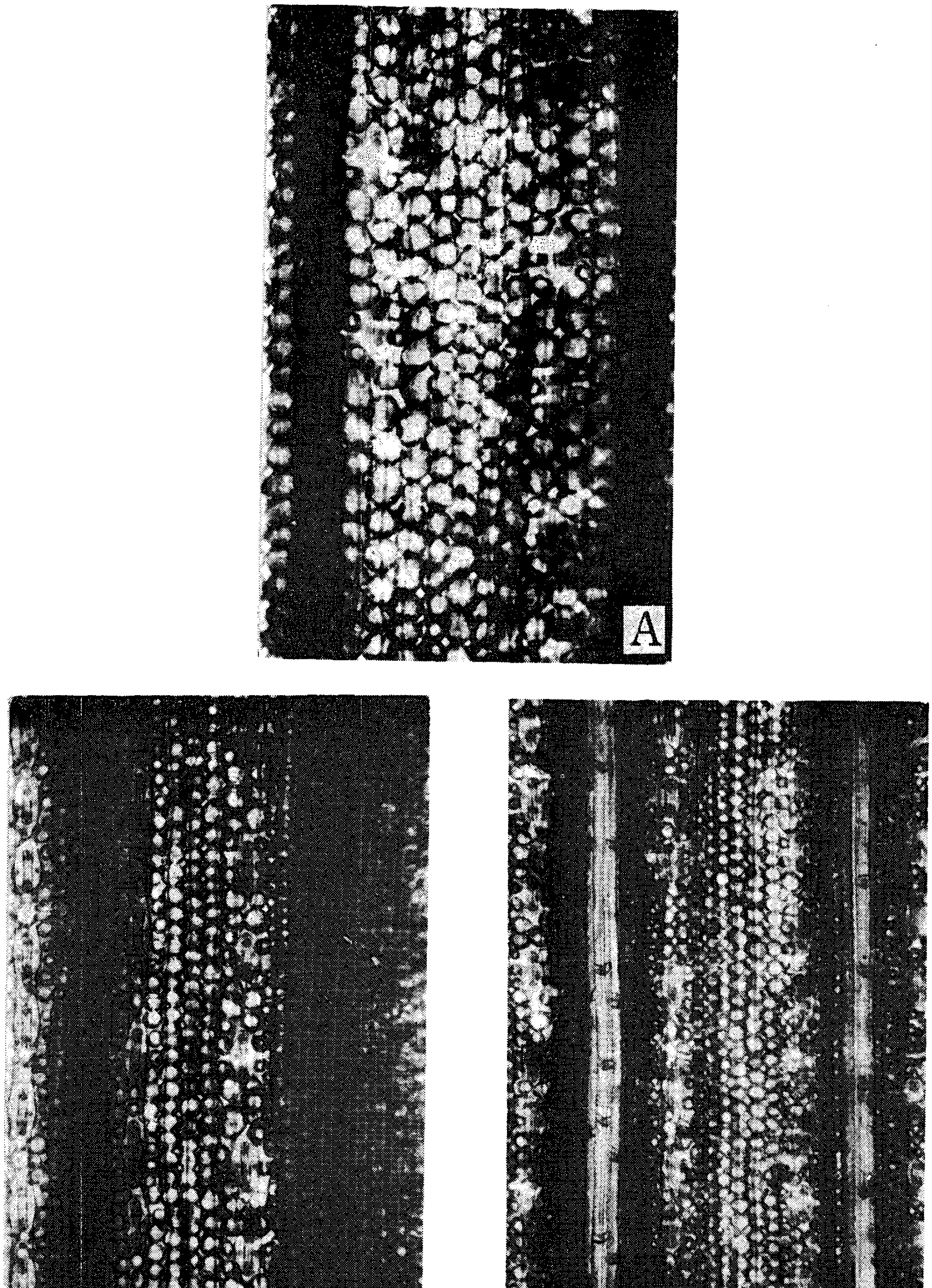

Plate 3. Mesophyll structure of the abaxial surfaces.

A, 5th leaf. B, 11th leaf. C, 13th (uppermost) leaf. A circular unit indicates a protuberance. The diameter of protuberances are decreased from the lower to the upper leaves. (All, × 90.)

several protuberances. The protuberance diameter measured at the base, at the middle and at the top of the leaf blades are shown in Table 1. In the leaf blades at lower levels, the protuberance diameter decreases from the base to the top of

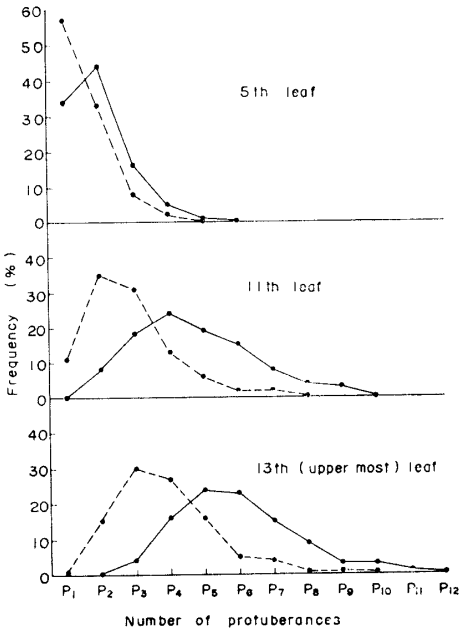

Fig. 2. Distribution of mesophyll cells possessed various numbers of protuberances.

—— : near the vascular bundles

---- : middle portions between the vascular bundles

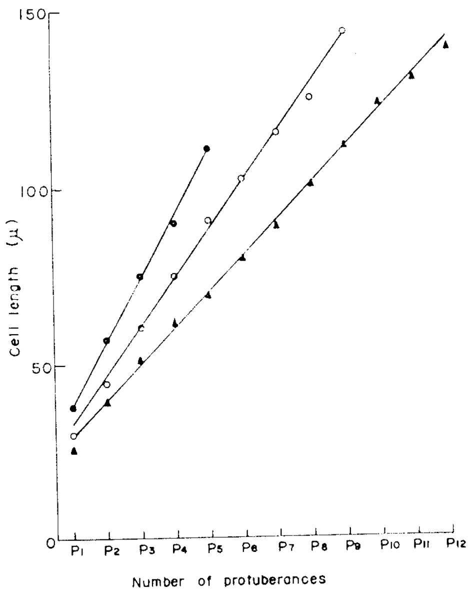

Fig. 3. Cell length (L)

●—● 5th leaf ○—○ 11th leaf ▲—▲ 13th (uppermost) leaf

leaf portions, on the other hand, such a obvious relation is not seen in the upper leaves. The protuberance diameter is slightly larger in the poritions near the midrib than in the edge of the leaf blades (Table 2).

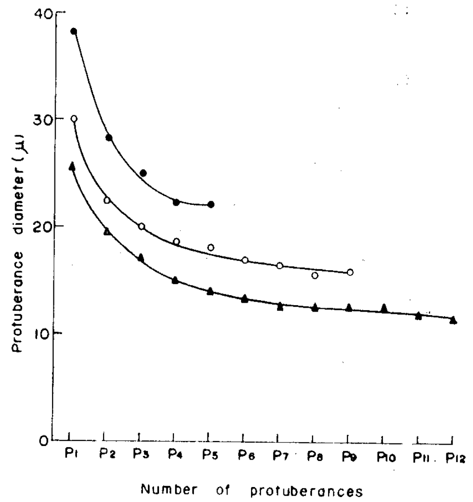

Fig. 4. **Protuberance diameter (r).**

Table 1. Leaf blade length and diameter of protubercances at the base, middle and top of portions in the leaf blade.

Leaf levels	Leaf blade length (cm)	Diameter of protuberance (μ)		
		base	middle	top
5th	8.6	42.3	35.3	37.5
8th	6.5	52.7	33.6	30.9
11th	14.2	25.8	23.0	21.7
13th	12.3	15.8	15.9	15.5

Table 2. Diameter of protuberances near the midrib and the edge of the leaf blade.

	5th	8th	11th	13th
Near the midrib	37.7 μ	35.9 μ	26.6 μ	17.2 μ
Edge of the leaf blade	32.9	31.4	21.0	14.7

As shown in Fig. 5, the cell width (W) varies in the range of $20\sim 50\mu$, and decreases as the number of protuberances increase. It has no definite relation among the leaves inserted at different levels, but in the 5th leaves it is inclined to have larger cell width.

As shown in Fig. 6, the protuberance length (l) varies from 7μ to 13μ, and decreases as the number of protuberances increase. There are no obvious difference in the protuberance length among the leaves inserted at different levels. The ratio of the protuberance length to the cell width (l/W), however, increase from the lower to the upper leaves, as shown in Table 3.

From the data of these observations, the cell surface (S) and the cell volume (V) were calculated by the following formulas, on the assumption that the column

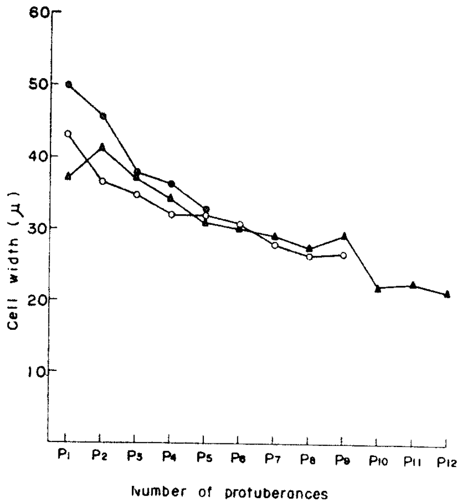

Fig. 5. Cell width (W).

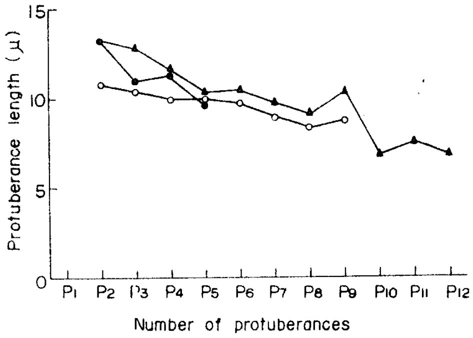

Fig. 6. ·Protuberance length (l).

Table 3. The ratio of the protuberance length to the cell width (l/W·%).

	P_2	P_3	P_4	P_5	P_6	P_7	P_8	P_9	P_{10}	P_{11}	P_{12}	Aver.
5th	29.1	29.1	31.1	29.5								29.7
11th	29.4	29.9	31.2	31.2	31.8	32.0	31.6	32.7				31.2
13th	32.2	34.7	34.1	33.7	34.5	33.9	33.6	35.4	30.6	33.6	32.0	33.5

shaped protuberances were placed on the both sides of a square shaped cell.

$$S = 2\left[(W - 2l)(L + r) + r(L + n\pi l)\right]$$

$$V = r\left[L(W - 2l) + \frac{n\pi rl}{2}\right]$$

The calculated surface and the volume of the cells are shown in Fig. 7 and 8 respectively. They increase as the number of protuberances increase, and the increase of the surface is larger than that of the volume, especially in the leaves at higher levels. The cells in the upper leaves have smaller surface and volume than those of the same number of protuberances in the lower levels. The ratio of the

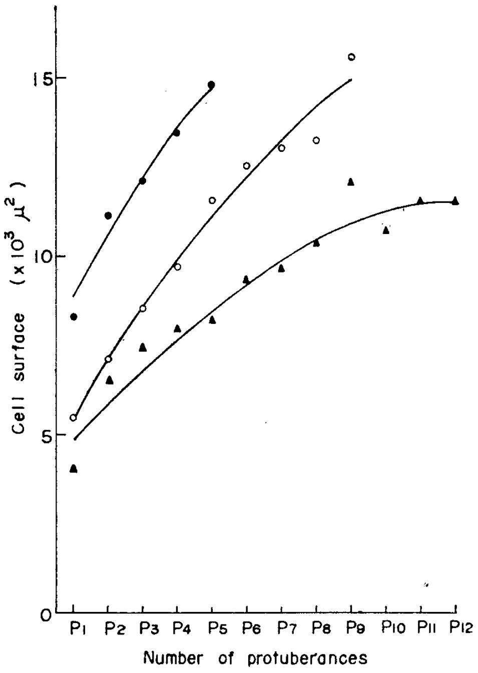

Fig. 7. Cell surface (S).

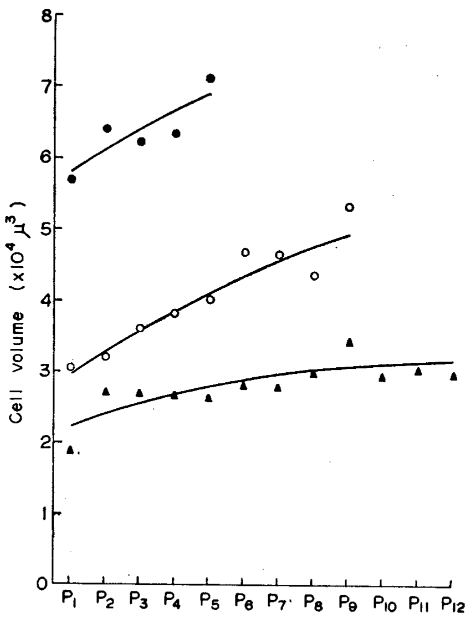

Fig. 8. Cell volume (V).

cell surface to the cell volume (S/V) increases as the number of protuberances increase, and also increase from the lower to the upper leaves (Fig. 9).

The number of cell layers in the middle poritions between the vascular bundles are commonly three in each levels of leaves. In these portions the number of cells per unit leaf area increase from the lower to the upper leaves. Therefore, the total

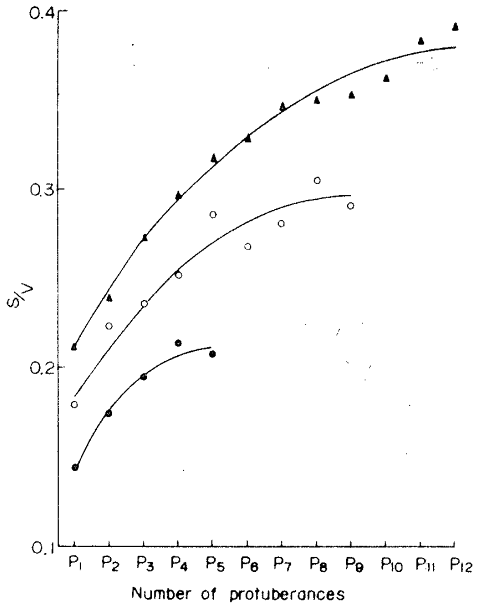

Fig. 9. The ratio of the cell surface (S) to the cell volume (V).

cell surface per unit leaf area increase in the upper leaves, although the average cell surface was decreased. The total cell surface is 17 to 25 times larger than the leaf area and the largest in the uppermost leaves (Table 4).

Table 4. Number of cells and cell surface per unit leaf area (1 mm²).

Leaf levels	Number of cells (N)	Average cell surface (S)	Total cell surface (N×S)
5th	1757	9643 μ^2	16.9×10^6 μ^2
11th	2233	8191	18.3×10^6
13th	3222	7757	25.0×10^6

Discussion

It was found that not only the chloroplasts invariably take up a peripheral position in a single layer along the cell wall, but also that they tend to spread over every protuberance of the wall. Therefore, the increase of the wall surface is not only effective to let the chloroplasts utilise the light as fully as possible, but also favourable to facilitates the gaseous interchanges associated with the photosynthetic function (3, 4).

Since the mesophyll has the morphologically developed arm-palisade cells and large cell wall surface, the upper leaves of wheat plant may have favourable structure for photosynthesis.

Maeda (6) has reported that the stomatal frequency increases from the base to the top of leaf blades at lower levels, on the other hand, such a obvious relation is not seen in the upper leaves. He has also indicated that the stomatal frequency increases from the lower to the upper leaves. Comparing the changes of the stomatal frequency with that of the protuberance diameter, it is suggested that the stomatal frequency increases as the total cell wall surface extend.

Turrell (7, 8) showed that the internal exposed surface of dicotyledon leaves may vary in different leaves on the same plant. The ratio of the internal to the external exposed surface was found to be relatively low in the shade leaves, intermediate in mesomorphic type, and high in xeromorphic sun leaves. In this study, although the extent of internal exposed surface were not measured, it is expected that the internal exposed surface may increase in proporition to the increment of the total cell surface. Accordingly, it seems that the upper leaves have a structure of xeromorphic sun leaves than the lower.

As shown in Table 1, the mesophyll structure of the 5th and 8th leaves resemble each other, but the structural difference between the 8th and 11th leaves are relatively greater. This difference may be related to some process of aging in the apcial meristem (1, 2). At the stage of double ridge formation, the elongation of the 8th leaf blade was almost ceased and the 9th and 10th leaf blades were in the midst of elongation. The leaf blades above the 11th, less than 3 mm in length, were elongated in the period of reproductive growth. However, each successive leaf was grown under the different environmental conditions. Therefore, the effect of temperature, light intensity, day length, soil conditions, etc. on the mesophyll structure of leaves should be investigated.

Summary

The meosphyll structure of the leaves at different levels of the main shoot of the wheat plants were observed.

In the leaves of the wheat plant, most of the mesophyll cells which are called the arm-palisade cells have several lateral protuberances developed at right angles to the leaf surface.

The diameter of protuberance, columnar or hemispheric in shape, is smaller in the upper leaves. In the leaves at lower levels, the protuberance diameter decreases from the base to the top of leaf protions, on the other hand, such a obvious relation is not seen in the upper leaves.

There are no obvious differences in the protuberance length among the leaves inserted at different levels, but the ratio of the protuberance length to the cell width increase from the lower to the upper leaves.

The average cell length of the upper leaves is longer than that of the lower, and there are positive linear relationships between the number of protuberances and the cell length as far as the leaves in the same level are concerned.

The ratio of the cell surface to the cell volume is raised as the number of

protuberances increase, and the number of cells per unit leaf area are increased from the lower to the upper leaves. Therefore, the total cell surface per unit leaf area is greater in the upper leaves, comparing with that in the lower leaves.

Generalizing from the observations in this study, it may be concluded that the upper leaves have a relatively more strongly developed arm-palisade tissue, probably more favourable for photosynthesis, than the lower leaves.

The author is indebted to Professor K. Wada for valuable advice and encouragement.

References

1) Ashby, E. (1948). New Phytol., **47**, 177.
2) Ashby, E. and E. Wangerman. (1950). New Phytol., **49**, 23.
3) Esau, K. (1953). Plant Anatomy. John Wiley & Sons, Inc.
4) Haberlandt, G. (1914). Physiological Plant Anatomy. London, Macmillan and Co.
5) Kaufman, P.B. (1959). Phytomorphology., **9**, 277.
6) Maeda, E. (1959). Proc. Crop Sci. Soc. Japan., **27**, 451.
7) Turrell, F.M. (1936). Amer. Jour. Bot., **23**, 255.
8) Turrell, F.M. (1942). Amer. Jour. Bot., **29**, 400.