

EFFECT OF THE INTENSITY OF ILLUMINATION ON THE DRY-MATTER PRODUCTION AND TISSUE STRUCTURE OF THE CAPSICUM SPECIES

† IMRE HORVÁTH, EDIT TAKÁCS and ERZSÉBET MIHALIK

Department of Botany, Attila József University, Szeged
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Abstract

Six different *Capsicum* species have been investigated in a phytotron to determine dry-matter production and the tissue structure of stem and leaf as a function of light intensity. Light energy was varied between $1.0 \cdot 10^4$ — $4.5 \cdot 10^4$ erg $\text{cm}^{-2} \text{sec}^{-1}$. It was established that:

1. The light demand of different species varies considerably, but there is no close connection between light demand and dry-matter production.

2. In general, leaf area changes with the intensity of illumination according to an asymmetric optimum-curve.

3. There is a significant positive correlation between the intensity of illumination and stoma number, as well as between the leaf cross-section and the epidermal cell count.

4. Dry-matter production shows a close positive correlation to the thickness of leaf-blade, the amount of spongy parenchyma and the xylem part of the vascular tissues of the stem.

5. From among the tissue areas of the stem, there is a significant negative correlation between the xylem part and the pith parenchyma.

Introduction

One of the important fields of interest of botanical research is the understanding of the many factors involved in the growth and development of plants. Among the environmental factors affecting this, light is of primary importance, being the energy supply for plant photosynthesis. The effect of light on tissue structure finds an expression through the external morphological properties of the plant. Tissue structure and morphology are often directly related to the production of organic matter.

In our experiments, we have dealt with the effects of different intensities of illumination on the morphological properties, the changes in the tissue structure of the stem and leaf, as well as the dry-matter production, of six *Capsicum* species.

Literary survey

Photosynthesis is considerably affected by several anatomical properties of plants, including the thickness of leaves, the structure of the assimilating parenchyma, and also by the proportion of vascular tissues. The relationship between tissue properties and organic production is not yet unambiguously established. The role of the spongy and palisade parenchymas in photosynthesis is particularly controversial. The same applies to the connection between morphological characteristics and the quantity of the photosynthetically produced dry matter.

BALLATTINE and FORDE (1970) investigated the tissue structure of the leaf of the soybean as a function of the intensity of illumination. A change was found in the structure of the spongy parenchyma: as a result of a greater light intensity the spongy parenchyma is more developed, showing an increase of 8 to 10 percent.

DARMANADEN et al. (1974) studied the connection between photosynthesis and the palisade and spongy parenchymas in the leaves of lettuce. These authors established that, in the spongy parenchyma, photosynthesis is more intensive and plastids differentiate, more quickly. Similarly, OUTLOW et al. (1976), measured the activity of some enzymes of CO₂ fixation in extracts of palisade and spongy parenchyma cells from the leaves of *Vicia faba*. In the cells of the spongy parenchyma enzyme activity is higher. Thus it may be concluded that, under identical conditions of illumination, CO₂ incorporation is greater in spongy parenchyma than in the palisade tissue. Opinions vary, however, in respect of the parts played by the spongy and palisade parenchymas in photosynthesis. One cause of this debate may be that the assimilating tissue functions in different ways, under different intensities of illumination. Such a result is known from OUTLOW's and FISCHER's investigations (1975) with *Vicia faba*. By increasing light intensity, photosynthesis increased in the palisade parenchyma, while in the spongy parenchyma it did not change.

NOBEL (1976) investigated the morphological and tissue characteristics of light and shade leaves. On increasing the intensity of illumination, the leaf-size decreased, leaf thickness increased and the palisade and spongy parenchymas were more developed. The greater photosynthetic activity was probably due, primarily, to the large inner surface of the leaf.

FRETZ and DUNHEM (1972) studies the connection between the intensity of illumination and the tissue structure of the leaves of *Ilex* species. Leaf area, leaf-blade thickness, and parenchymas all differed significantly as a function of illumination intensity, taken as a function of the intensity of illumination, generally changes according to an optimum-curve (BEAN, 1964).

Apart from the structure of mesophyll, stomatousness can also be connected with dry-matter production. Of all the tissue characteristics of the leaf, this factor responds to light most markedly.

KNECHT and O'LEARY (1972) ascertained that, under controlled conditions, at the epidermis of bean leaf, stoma-frequency significantly increased, as a function of intensity illumination. GAY and HURD (1975) obtained a similar result for tomatoes. Stoma-formation was retarded by a decrease in the intensity of illumination. The same phenomenon was observed by RAWSON and CRAVEN (1975) with tobacco and sunflower species.

HEICHEL (1971) called the attention to the connection between stoma-number and photosynthetic production of organic-matter. He established that in maize, photosynthesis is more intensive in leaves where the stoma-frequency is less.

FEKETE and SZUJKÓ—LACZA (1973) also found significant differences in the anatomical structure of leaves of *Quercus pubescens*, grown in four habitats of diverse water- and light supply. (Stoma-frequency, palisade and spongy parenchymas, rate of assimilating tissues and intercellular spaces). They have ascertained that the intensity of photosynthesis is altered according to the ratio of assimilating tissue to intercellular spaces and not by the stoma frequency. Light conditions also affect the vascular tissue system and, through this, the organic-matter production.

The activity of the cambium is increased by the increase in the intensity of illumination and, as a result of this, a more developed vascular tissue is formed (LEMAN 1955, JANKOVICH 1956, HORVÁTH 1965, SIMONNÉ—WOLCSÁNSZKY, SZEGEDI 1969, DENNE 1974).

Materials and Methods

The investigations were performed in the phytotron of the Botanical Gardens of the Attila József University (HORVÁTH 1972). Test plants were: 6 species of *Capsicum annuum*, namely: Javított cecei (Improved one from Cece), Magyar fűszer (Hungarian condiment), Cseresznye alakú (Cherry-shaped), Keszthelyi fehér (White from Keszthely), Szentesi fehér (White from Szentes), Paradicsom alakú zöld (Tomato-shaped green) Hungarian sorts. The experiment was repeated twice. The plants were grown in sand cultures and nutritive solution "KNOP" was used. The 70 percent water capacity was set on at the setting of the experiment, departing from air dry sand with nutritive solution. The permanent water content of the sand culture was preserved by watering it daily with distilled water on a weight basis. Once weekly, the plants were given an identical quantity of nutrient solution.

The daily temperature variation was between 20–25 °C. Air vapour content varied between 50–70%.

Illumination was provided by F₂₀-type fluorescent lamps of 40 watt (12 hours light, 12 hours dark). Different intensities of illumination were obtained by placing layers of tracing paper in front of the fluorescent tubes. The paper did not alter the spectral distribution of light energy. The following light treatments were applied:

4.5.10 ⁴ erg cm ⁻² sec ⁻¹	ca.	10.000 lux
3.5.10 ⁴ erg cm ⁻² sec ⁻¹	ca.	7.700 lux
7.10 ⁴ erg cm ⁻² sec ⁻¹	ca.	4.400 lux
1.5.10 ⁴ erg cm ⁻² sec ⁻¹	ca.	3.300 lux
1.0.10 ⁴ erg cm ⁻² sec ⁻¹	ca.	2.200 lux

In the following pages these light treatments are given with a coefficient of 10⁴ erg cm⁻² sec⁻¹.

The plants were processed at an age of 8 weeks. After being fixed at 105 °C, the dry weight was determined for each organ, by heating at 70 °C to constant weight.

For examination of organ structure, leaves were taken from node 3 and stems from internodium 4, from each of ten plants. For examination, preparations were made from the middle third of the leaf-blade.

The collected material was fixed in a mixture of ethylalcohol-formalin-distilled water, in the ratio of 3:1:1.

Epidermis was prepared by maceration, cleaned, stained with Ehrlich's acid haematoxylin, dehydrated, and then stabilized with Canada balsam.

For cross-sectioning, leaf and stem tissues were embedded in celloidin, and cutting with Reichert's slide microtome.

For studies on the epidermis, the epidermis cell, and stoma-numbers per unit area were determined for both epidermises. (As preparation from the average of 50 fields sight each).

From the leaf cross-section, leaf-blade thickness, the ratio of spongy to palisade parenchymas, and the size of cells were determined. From the cross-section of the stem, the ratio of the following tissue regions were determined: primary bark, xylem part, phloem part, mechanical tissue, pith parenchyma. The ratio of tissue regions was determined on the basis of the area of details drawn by means of a lanometer.

The examined tissue properties were analysed with t-test and correlation analysis (Sváb, 1973).

Results and Discussion

(a) Dry-matter production

Plants grown at low intensity of illumination (2200–3300 lux) had 8–10 leaves. Those grown at 7,700–10,000 lux had 12–12 leaves. No buds were visible.

Dry weights are summarized in Table 1.

Table 1

Species	light energy (10^4 erg cm^{-2} sec^{-1})				
	4.5	3.5	2.0	1.5	1.0
White of Szentes	609	626	441	308	154
Tomato-shaped	586	691	418	302	183
White of Keszthely	512	563	372	302	194
Improved from Cece	817	643	551	346	277
Hungarian condiment	498	492	457	436	346
Cherry-shaped	439	457	410	382	322

It is immediately apparent that dry-matter production and light demand of individual species are considerably different. There is no obvious connection between light demand and the dry-matter production: the dry matter of the least light-demanding capsicum species, the tomato-shaped one, is the third in sequence. The most light-demanding species is the improved one from Cece.

The light-curves reflecting the light demand are shown in Fig. 1.

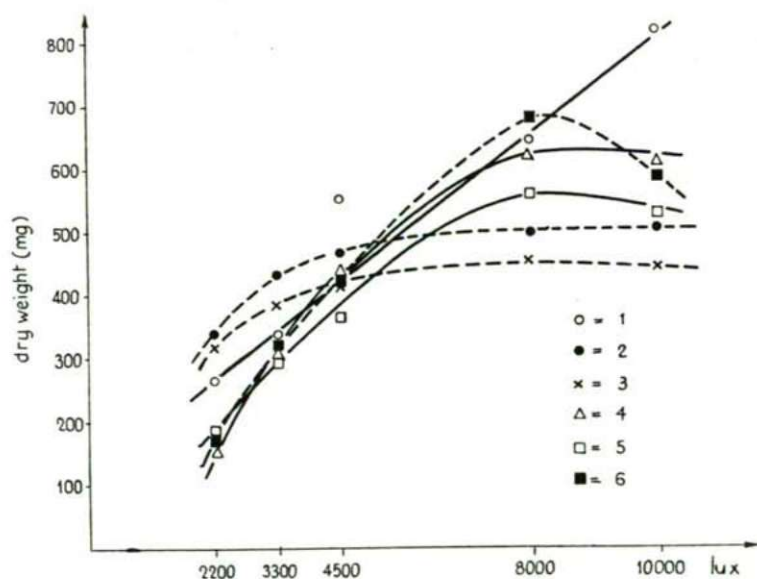


Fig. 1. Dry weight of capsicum species, as a function of the intensity of illumination (light-curves).

It can also be shown that in general the more light-demanding a species is, the larger is the weight difference as a function of the intensity of illumination. Similar results are mentioned by BAROOVA—HORVÁTH (1973) and BERNÁTH (1976).

From among the morphological properties, we shall only discuss leaf area, because this factor is generally most closely related to dry-matter production.

Variation in leaf area for each species was considerable being more than 100

percent. (The largest and smallest leaf areas calculated for one plant are 512 and 252 sq. cm, respectively). There was no direct proportionality between light-demand and leaf-area.

In general, leaf are changed together with the intensity of illumination, according to an asymmetrical optimum-curve. With two species, under our experimental conditions, leaf area was practically unchanged, as a function of the intensity of illumination. The Cherry-shaped species gave the most marked response: the difference between the smallest and largest leaf areas being five-fold (Fig. 2.)

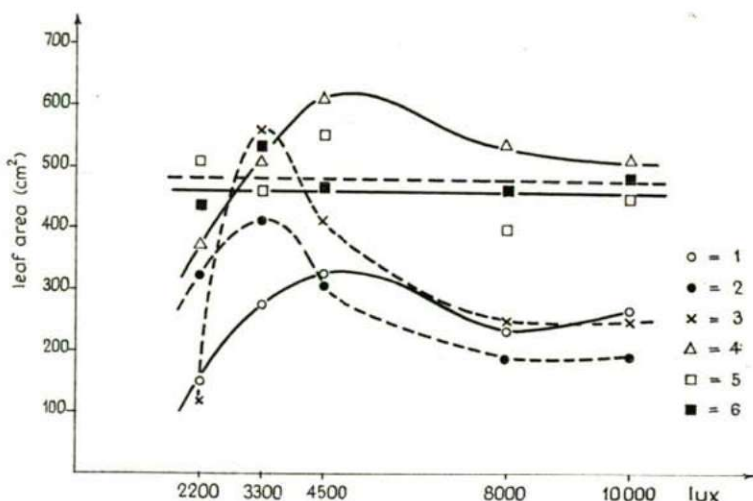


Fig. 2. The average leaf area of *Capsicum* species calculated to one plant, as a function of the intensity of illumination.

Our data also show, that maximum leaf area was formed at about 3–4,000 lux, and did not change with light intensities up to 8–10,000 lux. This result was obtained with all the species tested.

Our results are in agreement with the earlier results of HORVÁTH (1965), as well with those of COOPER and TAINTON (1968) and BERNÁTH (1976), according to which, leaf area is increased within limits by lower light energy levels.

These results also support Bean's statement (1964), that leaf area generally changes as a function of illumination intensity according to an optimum-curve. The percentage of the total dry weight represented by the leaf is larger with species of higher light-demand (KUDRYAVSTEV, 1964; Mc. WORTHER-JORDAN, 1976). Among different *Capsicum* species the fraction of the dry weight represented by the leaf may vary by some 10–20 percent.

The result of our histological investigation (Plates 1, 2, 3) are summarized below that, in general we were analysing the correlation between the tissue properties the intensity of illumination, and the dry-matter production.

The epidermal cell count per unit area increased, particularly on the lower epidermis, in parallel with the intensity of illumination. The connection is strong, the correlation coefficient is also significant at level $r = +0.96$ and p 5 percent (Fig. 3).

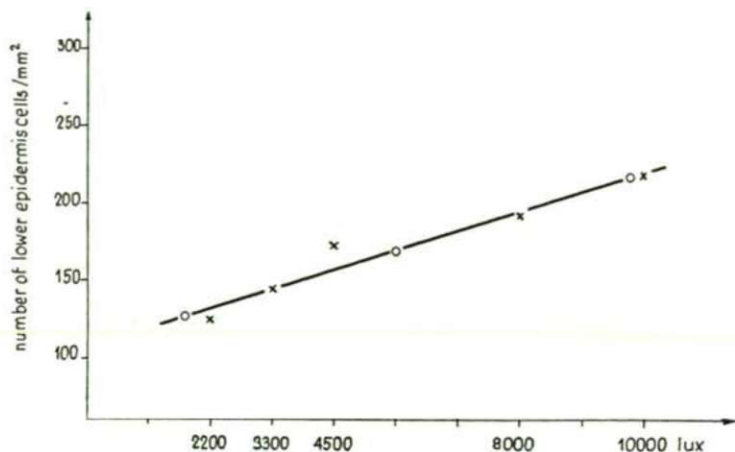


Fig. 3. Connection between the cell count of the lower epidermis (piece/sq. mm) and light energy on the basis of the mean values of the 6 capsicum species.

The difference of cell counts between the two extreme intensities of illumination is significant even at level p 1 percent.

The leaf of *Capsicum* is amphistomatic; the number of stomata is some 5–6 times lower at the upper surface, than at the lower epidermis. The formation of stomata was, however, considerably inhibited, particularly on the upper epidermis, by a decrease in the intensity of illumination. Under such conditions the leaf became almost hypostomatic. (1 piece) sq.mm stoma contra 10–35 piece (sq.mm). A similar tendency may be observed at the lower epidermis (Fig. 4).

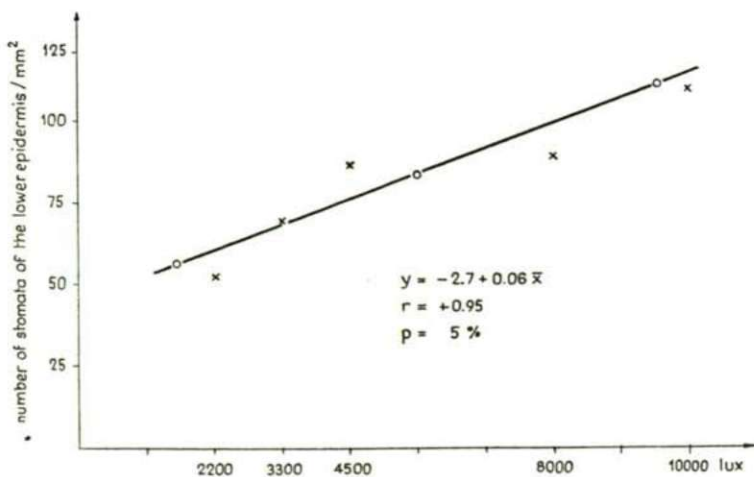
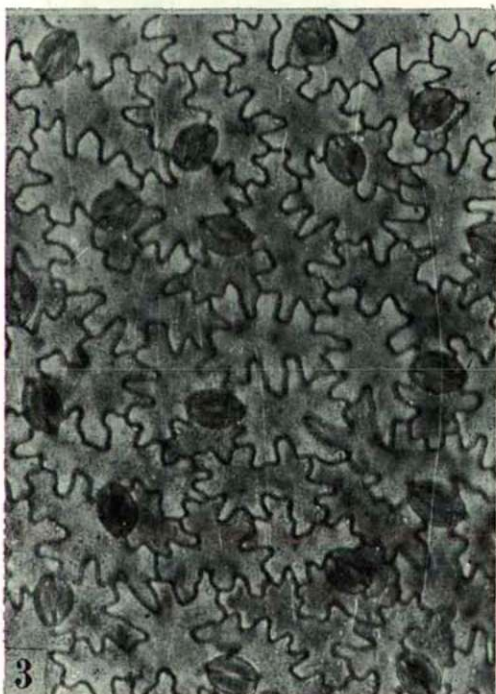
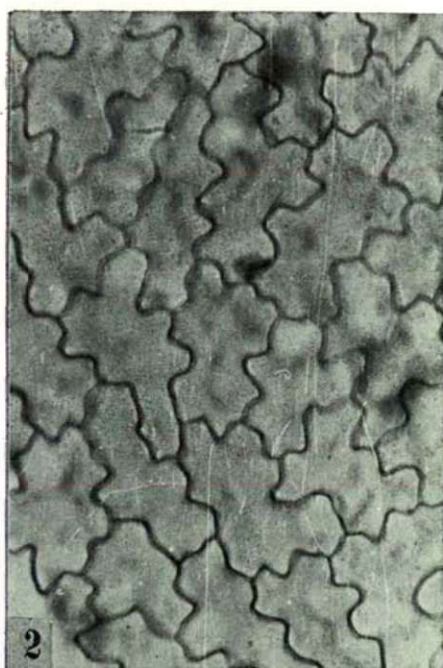
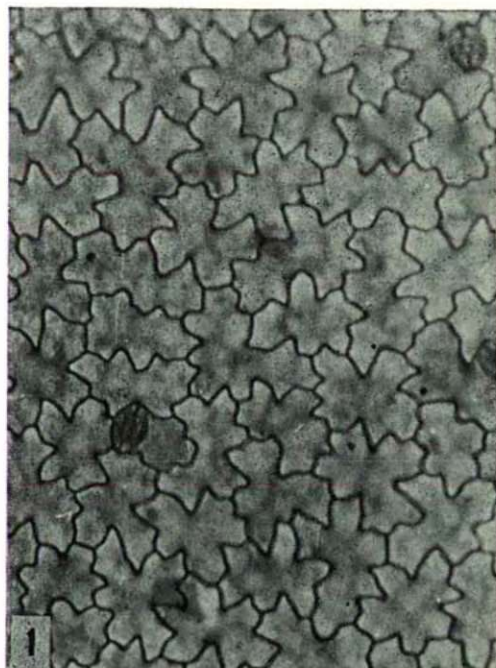


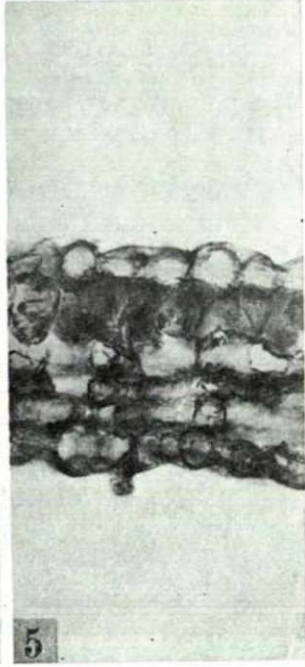
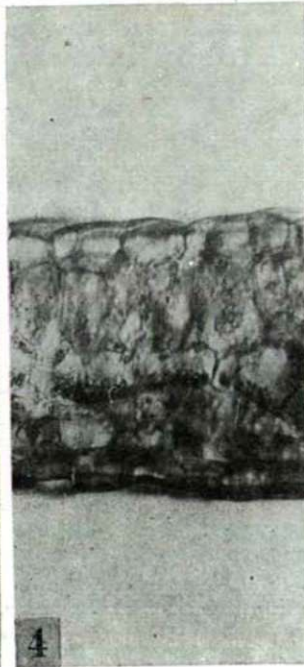
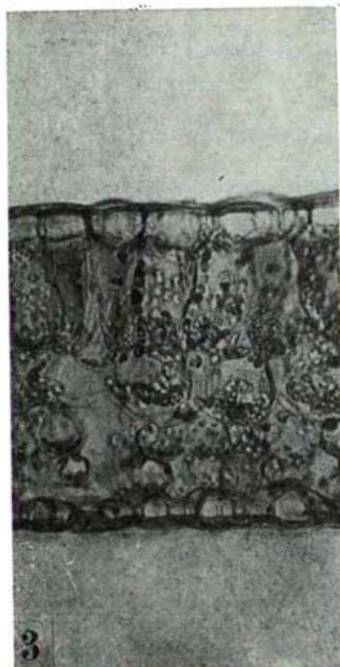
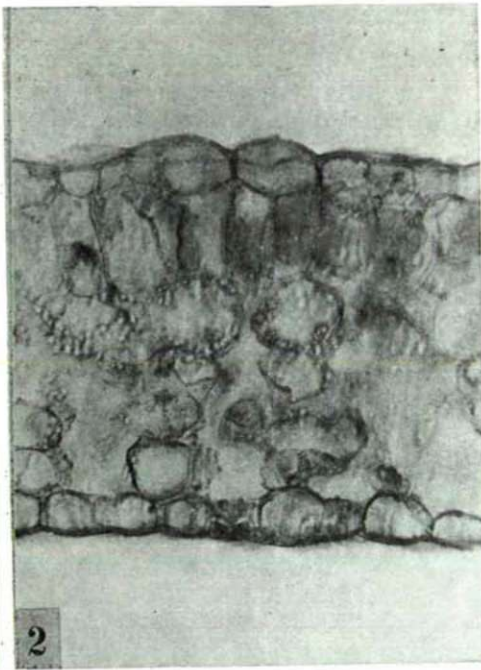
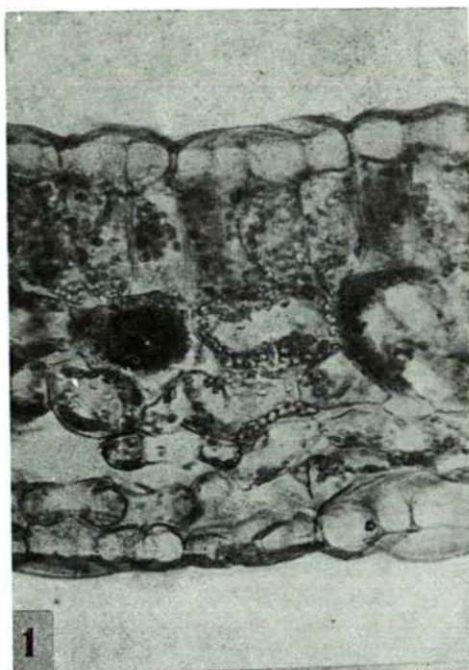
Fig. 4. Connection between the stoma number of the lower epidermis (piece/sq. mm) and light energy, on the basis of the mean values of 6 *Capsicum* species.



Capsicum annum L. c. v. White of Keszthely
1. upper epidermis 10.000 lux (250 x).
2. upper epidermis 2.000 lux (250 x).

3. lower epidermis 10.000 lux (250 x).
4. lower epidermis 2.000 lux (250 x).

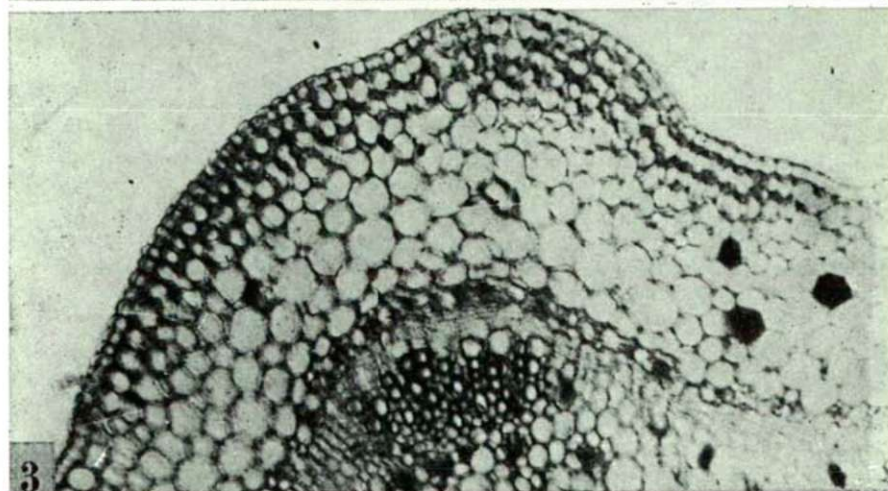
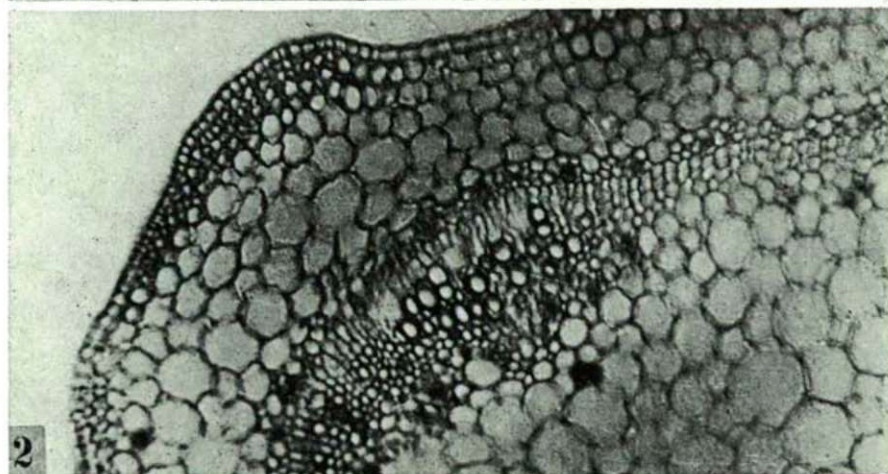
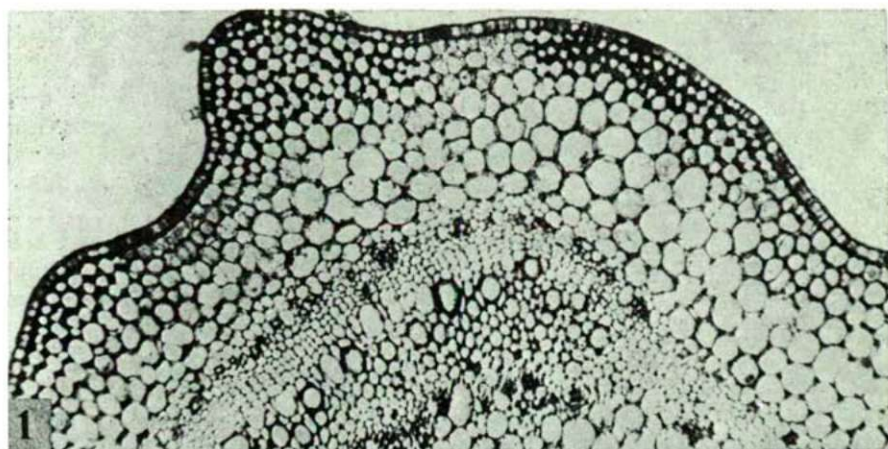
Plate II



Capsicum annum L. c. v. Improved from Cece, leaf cross section

1. 10.000 lux (250 x).
2. 8.000 lux (250 x).
3. 4.500 lux (250 x).

4. 3.000 lux (250 x).
5. 2.000 lux (250 x).



Capsicum annuum L. c. v. Tomato shaped green. stem cross section.
1. 10.000 lux (85 x) 2. 8.000 lux (85 x) 3. 3.000 lux (85 x).

There was no significant correlation between stoma number per unit area and dry weight.

According to FRANK (1969) and HEICHEL (1971), the stoma frequency decreases in parallel with the increase in the photosynthetic productivity. From our investigations, the connection is not close. We agree, however, with FEKETE and SZUJKÓ (1973), that dry-matter production is modulated, in some way, only by the inter-cellular spaces. NOBEL (1976) emphasizes that greater photosynthetic activity is induced by a larger inner surface of the leaf.

The correlated, parallel changes between the thickness of the leaf-blade and the intensity of light are generally known. The correlation is close, according to our investigations. It is significant at $r = +0.94$ and at 5 percent level (Fig. 5).

The improved species from Cece was most sensitive to changes in light intensity, the extremes of leaf thickness differed by 100%. The thickness of the leaf of less light-demanding species changed to a lesser extent.

There is a close correlation between thickness of the leaf-blade and dry weight. The value of r is $+0.96$ and the connection is significant at $p = 1$ percent level (Fig. 6).

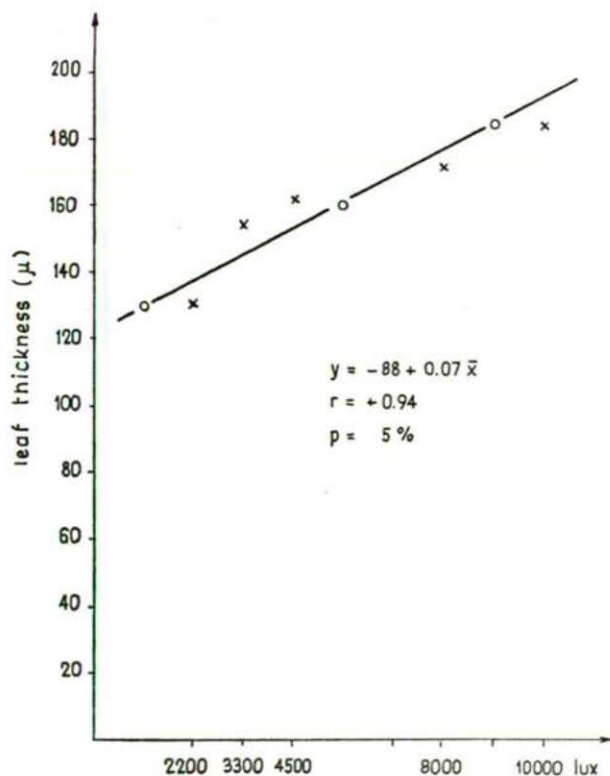


Fig. 5. Connection between the thickness of leaf-blade and light energy, on the basis of the mean values of the six *Capsicum* species.

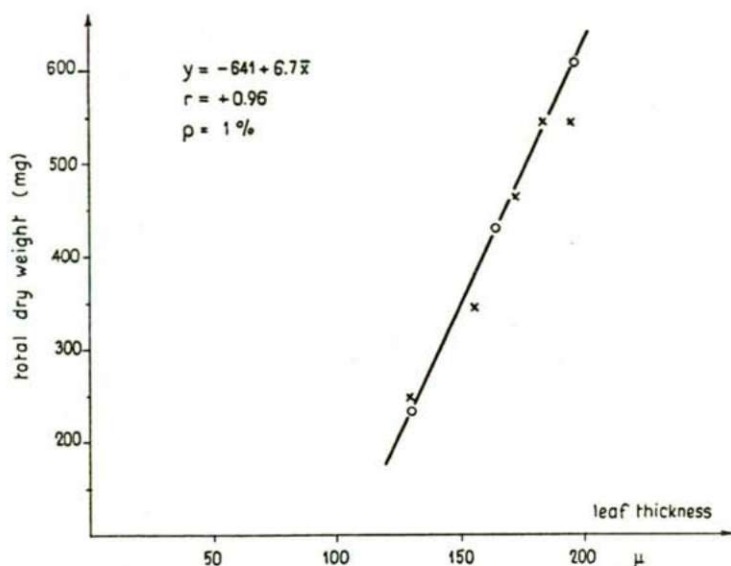


Fig. 6. Connection between the dry weight and the thickness of the leaf-blade, on the basis of the mean values of the six capsicum species.

The effect of the intensity of illumination on the assimilating parenchyma is considerable, too. This effect appears in the spongy parenchyma. The amount of the spongy parenchyma increases as a function of the intensity of illumination. The connection is close, it is significant at the level of $r = +0.98$ and $p = 1$ percent (Fig. 7).

We remark that the extreme values appearing in the development of the spongy parenchyma significantly differ from one another at the level $p = 0.1$ percent, as well. The parts played by the spongy and palisade parenchymas in photosynthesis is often debated. According to our data, in the case of Capsicum, the increased photosynthetic role of the spongy parenchyma is proved by the increased production of organic matter. Similar conclusions are also drawn by a number of other research workers, e.g., STARZECKI, 1962; BALLANTINE—FORDE, 1970; DARMANADEN et al., 1970; OUTLOW et al., 1976.

From among the tissues of the stem, the development, of mechanical tissues bears a close positive correlation with intensity of illumination. The difference between the extreme values is significant at $p = 0.1$ percent level. The percentage of mechanical tissues varied in our investigations between 6 and 10 percent. The most striking phenomenon is the different development of the xylem part of vascular tissues. This shows a close positive correlation with the intensity of illumination and is significant at $r = +0.90$ and at $p = 5$ percent level. Even more striking is the connection between the development of xylem tissue and the dry matter. Again, this a positive correlation and significant at $p = 0.1$ percent level (Fig. 8).

In the phloem part of vascular tissues the difference is much less pronounced and is only significant between the two extreme intensities of illumination $p = 5$ percent.

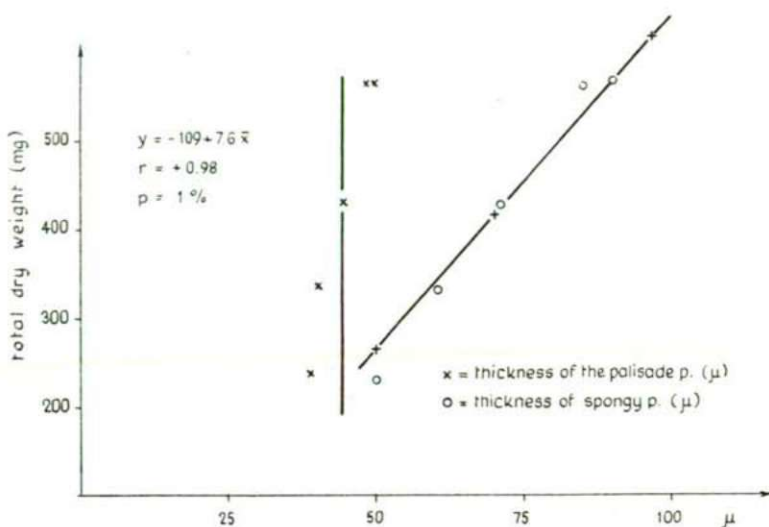


Fig. 7. Connection between the total dry weight and the thickness of the spongy, resp. palisade parenchyma, on the basis of the six *Capsicum* species

x = thickness of the palisade parenchyma
o = thickness of the spongy parenchyma.

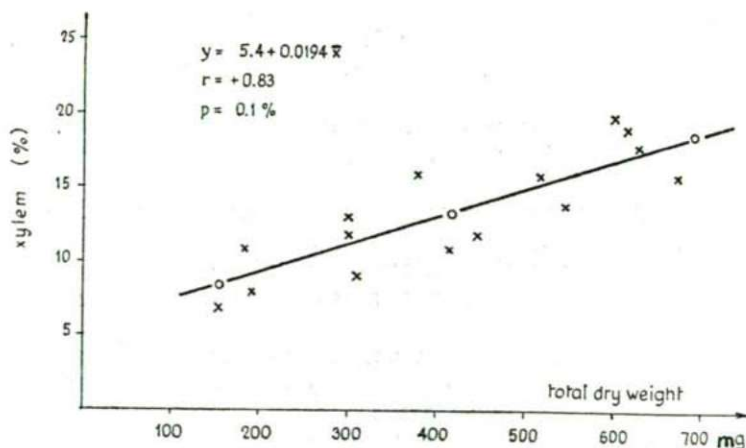


Fig. 8. Connection between the total dry weight and the percentage of the xylem part (stem), on the basis of the Tomato-shaped, White from Keszthely and White from Szentes capsicum species.

Of tissue areas of the stem the pith parenchyma changes considerably. This decreases, as a function of the intensity of illumination, significantly at $r = -0.92$ and $p = 5$ percent.

The change in the tissue area is, therefore, contrary to the change in the xylem part of the vascular tissue and the reliability of the connection is significant at p 1 percent level (Fig. 9).

We have earlier indicated such a connection (HORVÁTH, 1965) and a number of similar results have been reported (LEMAN, 1955; JANKOVICH, 1956; Mrs. SIMON and SZEGEDI, 1960; GULYÁS et al., 1970; TAKÁCS, 1973).

In Tables 1–3. the changes induced in the epidermis, the tissue structure of the leaf, and the stem are demonstrated.

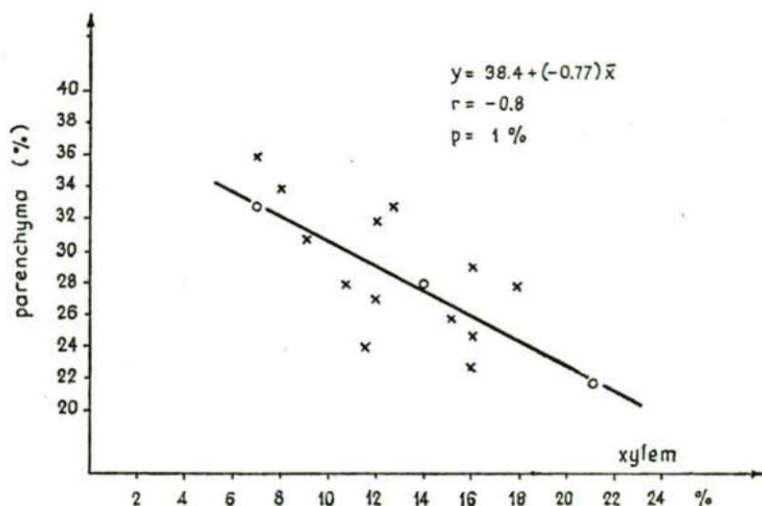


Fig. 9. Connection between the percentage of pith parenchyma and xylem part, on the basis of the Tomato-shaped, White from Keszthely and White from Szentes species.

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Address of the authors:

† Prof. Dr. I. HORVÁTH

Dr. EDIT TAKÁCS

Dr. ERZSÉBET MIHALIK

Department of Botany, A. J. University

H—6701 Szeged, P. O. Box 428

Hungary