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The relationship between anatomical and morphological characteristics of green tomato fruit and their susceptibility to late blight (*Phytophthora infestans* (Mont.) de Bary)

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Abstract

The purpose of the studies carried out in 1983-1985 was to determine the relationships between the degree of susceptibility of green tomato fruit to late blight and several of the anatomical and morphological features of these fruits. It was found that in the studied material representing a wide range of susceptibility (from various degrees of resistance to susceptible) the extent of infection was dependent on the covering layer thickness (with cuticle) and number of hairs on the skin.

INTRODUCTION

One of the components of horizontal resistance of plants to infectious diseases is passive resistance which, in turn, is made up of factors inhibiting or hindering the penetration of the pathogen into the susceptible plant tissues (Kochman, 1973). One of these factors is the biochemical and physical structure of the surface of the plant organ. The reaction to a specific type of surface called thigmotropism or contact-tropism plays an important role in the pre-infection stage. Influencing thigmotropism does not guarantee full resistance, but does reduce the infection rate of plants (Winn and Staples, 1981). According to Kochman (1973) important factors hindering infections are the wax layer, thick epidermis and cuticle. Cooper (1981) considers the cuticular wax to be the most important barrier in the pre-infection stage of disease development.

A pathogen usually penetrates into tomato fruits through the sepals, mechanical injuries to the skin (Reed, 1912; Melhus, 1916; Milbrath, 1928; Roder, 1935; Kochman, 1973) or through undamaged skin (Kubicka, 1969; Eggert, 1970). In the case of certain fungal pathogens, such as *Botrytis cinerea*, an important factor in their penetration into tomato fruit is the skin and cuticle thickness (Gaumann, 1933; Kochman, 1973) (Fig. 1 according to Gaumann (1951)).

According to Chebanu (1972), the skin of green tomatoes is made up of an epidermis covered with a cuticle and wax layer and by a hypodermis. The

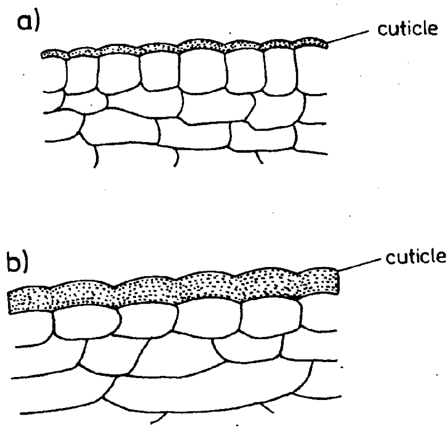


Fig. 1. Cross-section of tomato fruit covering layer a — susceptible fruit, b — resistant fruit after infection by *Botrytis cinerea* (Gaumann, 1951).

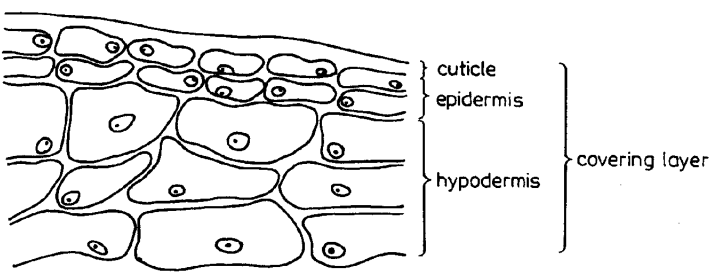


Fig. 2. Diagram of the measured covering layer of green tomato fruit

epidermis is one row of elongated cells (Fig. 2). After examining several score tomato cultivars Chebanu found that there may be two types of cuticle. In the cultivars bearing large fruits the cuticle usually penetrates inbetween the lateral walls of epidermal cells, whereas in the small fruit varieties, it penetrates deeper through the epidermis even reaching inbetween the lateral cell walls of the hypodermis. The cuticle thickness usually falls between 5 and 12 μm. Depending on the variety, the hypodermis may have a variable thickness. The fruit from large fruit varieties has a hypodermis made up of 2-3 cell layers, while of small fruit varieties, of 3-6 layers.

Some authors distinguish three parts in the structure of tomato fruit: the exocarp, mesocarp and endocarp. They call the excarp, that is, the cuticle and epidermis, the skin (Chu and Thompson 1972a, b). Others, however

(Pearson, 1970; Kozhevnikova and Dorozhkina, 1971), speak only of the covering layer of the fruit, made up of the cuticle, epidermis and subepidermis.

Rosenbaum and Sando noticed the importance of the thickness of the covering layer in the process of infection when they compared the development of the fungus, *Alternaria porri* F. sp. *solani*, on various tomato fruits and found a correlation between the resistance of the fruit and the thickness of this layer (Gaumann, 1933). A similar correlation in respect to resistance to potato blight was found by Kozhevnikova and Dorozhkina, (1971) upon measuring the thickness of the particular tissue layers covering green fruit. The only significant differences which they found between the resistant and susceptible fruit was in the thickness of the cuticle which equalled 5-6.5 μm in the resistant and 3.4-4.1 μm in the susceptible ones. According to these authors, cuticle thickness may be used to determine field resistance.

On the basis of the fact that unripe fruit is more easily infected than ripe fruit, Kubicka (1969) suggested that the thickness of the whole skin plays a role in the process of infection. Eggert (1970) presented the opposite opinion, claiming that the thickness of the skin and cuticle are of no importance in the resistance of fruit to *Phytophthora infestans*. In all certainty, this role cannot be played by stomas, of which there are very few in the skin of fruits from the nightshade family (Kaniewski, 1965; Ważynska, 1967).

Numerous species with hairy fruits have been found in the genus *Lycopersicon*. "Woolly" mutants (Rick, 1955) have been found in crop varieties, and several "woolly" lines of tomatoes have been obtained (Lesley et al., 1966), overcoming the lethal effect of gene Wo which determines hairiness (Sawant, 1955).

The objective of the studies conducted in 1983-1985 was to search for relationships between the degree of susceptibility of tomato fruit to late blight and some of their anatomical and morphological characteristics.

MATERIAL AND METHODS

The studies were carried out on green, field-grown tomato fruit from Reguły. Three series of infection experiments were done on the fruit of 47 varieties and breeding lines differing in respect to their resistance. The susceptible varieties were represented by Moneymaker and Rutgers, resistant ones by West Virginia 700, No. 155/84 and No. 62/74. The experiments were conducted in 10 replicates, taking 9 fruits in each. The fruits were taken at random, one from the first cluster of each plant and subjected to infection in an infection chamber where optimum temperature, humidity and lighting for the development of the fungus were maintained. After sterilization, they were arranged on damp filter paper in containers with transpartent tops. The fruit was infected by instilling a highly pathogenic inoculum at a concentration of

50000 conidiospores per cm^3 of suspension on the calycine depression with the sepals left in place.

The degree of infection of the fruit was evaluated according to the method given by Horodecka (1989). The green fruit of the same varieties and lines was collected for examination of the following anatomical and morphological characteristics: size of calycine depression, covering layer thickness, cuticle thickness and number of hairs. These traits were determined at the same time as the infection experiments were being conducted.

DETERMINATION OF THE CALYCINE DEPRESSION SIZE

The diameter of the calycine depression in its widest point was measured with an accuracy of ± 1 mm using a compass and ruler.

The calycine depression size index, K, was calculated according to the following formula

$$K = \frac{\text{calycine depression diameter}}{\text{transverse diameter of the fruit}} \times 100\%.$$

MEASUREMENT OF THE COVERING LAYER THICKNESS

The thickness of the covering layer was measured using a microscope and micrometer (Broda, 1971). The measured layer was composed of: the cuticle, epidermis and several layers of hypodermis cells (Fig. 2).

The samples were taken from green, good-sized fruit, collected from the same position in the cluster as those used for inoculation (1 fruit per first cluster of each plant). Samples of the pericarp used in making the slides were taken from three places on the fruit: the calycine depression, the middle part and next to the trace from the pistil. The samples were placed on the pith of a lilac stem (longitudinal section). Cross sections were then made through the stem with a microtome blade, sectioning the pericarp at the same time (Broda, 1971).

Three slides were made from each place on the fruit, and 3 microscopic measurements were made on each slide. Cuticle measurements were made separately on material taken from an area close to the calyx. The slides were stained immediately after preparation with a saturated solution of Sudan III, washed with 50% ethanol, distilled water and sealed in glycerol (Broda, 1971). The degree to which the cuticle penetrated into the covering layer was also observed.

DETERMINATION OF THE NUMBER OF HAIRS ON THE FRUIT

The number of hairs was determined using a stereoscopic microscope by examining a sample taken from an area near the calyx and counting the number of hairs on a 1 cm^2 area. Due to the laboriousness of this technique, in

1985 it was changed and the number of hairs was estimated according to the following scale:

0 – lack of hairs,
1 – single hairs,
2 – over 10 hairs,
3 – over 25 hairs,
4 – over 50 hairs,
5 – over 100 hairs.

STATISTICAL ANALYSIS OF THE RESULTS

Linear regression and correlation of pairs, as well as mulitple regression and correlation analysis methods were applied in the statistical assessment of the obtained data. The traits used in the regression equations were introduced by an self-selection method. The significance of the differences was evaluated at $\alpha = 0.05$. The calculations were carried out on an Odra 1305 computer at the Institute of the Fundamentals of Information Theory, Polish Academy of Sciences.

RESULTS

The results of the infection tests allowed the studied cultivars and breeding lines to be classified into 4 groups based on their degree of infection:

A – very weak infection,
B – moderate degree of infection,
C – strongly infected,
D – very strongly infected.

When the variability of the various anatomical and morphological traits of these groups of cultivars and breeding lines was analysed, it was found that they differed significantly among themselves in respect to covering layer thickness in the upper fruit part, cuticle thickness, number of hairs and size of calycine depression (Table 1). Non-significant differences were observed in the covering layer thickness in the middle and lower fruit parts. The characteristic anatomical and morphological traits in the moderately and strongly infected varieties and lines differed distinctly from these traits in the weakly infected group (Table 1).

In the first series of experiments when only the covering layer thickness was measured, a relationship between the thickness of this layer in 3 places on the fruit and the size of the spot was found. The area of the spot decreased proportionally to the increase in covering layer thickness (Fig. 3).

In the second series where, in addition to covering layer thickness, the remaining anatomical and morphological characteristics were examined, it was

Table 1

Statistical characterization of anatomical and morphological features of tomato fruit in different

Fruit infection	Covering layer thickness of fruit								
	carpel			middle part of fruit			basin		
	$\bar{x}$	S	$V\%$	$\bar{x}$	S	$V\%$	$\bar{x}$	S	$V\%$
A	145.42	62.53	43.00	131.97	61.38	46.51	132.61	55.16	41.60
B	121.77	62.65	51.45	104.36	49.81	47.72	120.67	55.74	46.19
C	115.50	54.42	47.11	106.30	50.75	47.74	114.74	55.65	48.50
D	114.77	56.00	48.80	100.57	44.38	44.13	109.52	50.57	46.17
Test q	A	A C D		A	B C D		A	B C D	

A – weak infection, B – moderate infection, C – strong infection, D – very strong infection.

found that there are various correlation coefficients for various infection indicators (infection after 4 days, spot, fur, streaking) and anatomical and morphological traits (Table 2). And so, for infection 4 days following inoculation, almost all of the calculated coefficients were found to be significant, while for spot size, only those coefficients pointing to a connection with the number of hairs, covering layer thickness of the lower part of the fruit and cuticle thickness were significant. There were even fewer correlations between mycelium fur and other traits. Of the 48 studied correlations, 28 were found to be significant. Of these, the strongest correlation was found between infection 4 days after inoculation and the number of hairs ($r = -0.81$) and with the covering layer thickness ($r = -0.50$ to -0.68) (Table 2). The relationships among the studied traits are shown on Figure 4.

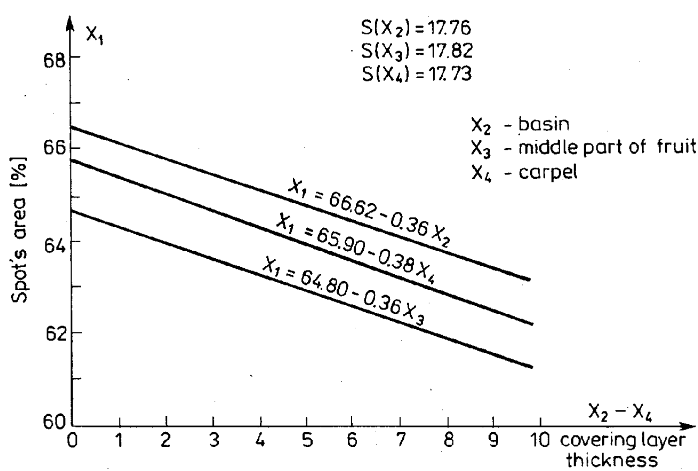


Fig. 3. The relationship between late blight infection and covering layer thickness of tomato fruits

groups of degrees of infection by the fungus, *Phytophthora infestans*

Cuticle thickness			Number of hairs on the skin			Size of calycine depression *K*		
$\bar{x}$	*S*	*V*%	$\bar{x}$	*S*	*V*%	$\bar{x}$	*S*	*V*%
10.56	6.17	58.43	178.70	90.81	50.82	14.34	4.93	34.41
9.01	4.05	44.94	126.72	93.20	73.55	16.74	5.82	34.75
7.51	3.78	50.29	101.02	93.98	93.03	18.15	5.38	29.65
8.01	3.24	40.42	102.29	97.02	94.85	17.66	5.60	31.74
A	A C D		A	B C D		A	B C D	

Similarly as in series two, in series three the strongest correlation was found between infection 4 days following inoculation and covering layer thickness ($r = -0.67$) as well as between spot size and streaking with the size of the calycine depression ($r = 0.66$ and $r = 0.69$). It was also found that, of the

Table 2

Correlations between pairs of anatomical and morphological features and fruits' infection – set 2 ($R_{tab.} = 0.29$)

	1	2	3	4	5	6	7	8	9
2	0.34*								
3	−0.38*	0.09							
4	0.24	0.41*	−0.08						
5	−0.02	0.20	0.01	0.30*					
6	−0.81*	−0.33*	0.35*	−0.31*	−0.10				
7	−0.68*	−0.31*	0.35*	−0.33*	−0.23	0.69*			
8	−0.54*	−0.17	0.21	−0.26	−0.17	0.61*	0.86*		
9	−0.50*	−0.11	0.21	−0.11	−0.25	0.55*	0.80*	0.80*	
10	−0.32*	−0.35*	0.19	−0.36*	−0.34*	0.42*	0.60*	0.52*	0.49*

1 – infection after 4 days, %,
2 – spot after 14 days, %,
3 – fur after 14 days, %,
4 – fruits' streaked with mycelium, %,
5 – amount of calycine depression *K*, %,
6 – hairs' number in cm^2,
7 – covering layer thickness – basin,
8 – covering layer thickness – middle part of fruit,
9 – covering layer thickness – carpel,
10 – cuticle thickness.

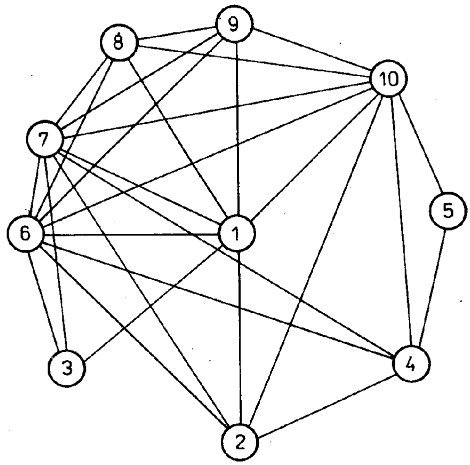


Fig. 4. Relationships between the anatomical and morphological features of tomato fruits and different types of infection by *Phytophthora infestans*

1 – Infection after 4 days; 2 – Spot after 14 days; 3 – Fur of mycelium; 4 – Depth of pericarp streaked with mycelium; 5 – Calycine depression area *K*; 6 – Number of hairs/cm^2; 7 – Covering layer thickness – basin of fruit; 8 – Covering layer thickness – middle part of fruit; 9 – Covering layer thickness – carpel; 10 – cuticle thickness

studied fruits, the thickest cuticles were in the resistant West Virginia 700 line (10.04 μm), No. 62/74 (5.70 μm) and in the partially resistant varieties Goniec (5.70 μm) and New Yorker (5.60 μm), while the susceptible variety, Moneymaker, had the thinnest cuticle (1.09 μm).

The relationships between the studied anatomical and morphological traits of fruit and the degree of their infection with the fungus, as found by multiple regression and correlation analysis, were differentiated and dependent on the infection index (Table 3). The greatest influence on fruit infection 4 days following inoculation was found for the number of hairs on the fruit skin (coefficient of partial correlation $R = -0.69$ at $R_{tab,}$ -0.29). A significant, albeit lesser effect, was of the covering layer thickness at the calycine depression ($R = -0.30$). The cuticle thickness had a significant effect on the size of the spot 14 days after inoculation and extent to which the pericarp was streaked with mycelium, ($R = -0.35$) while the size of the fur was significantly influenced by the thickness of the covering layer at the calycine depression ($R = 0.35$).

Multiple correlation analysis also showed a mutual relationship between various indicators of fruit infection. The spot size was most strongly correlated with the streaking with mycelium ($R = 0.37$). The size of the fur was dependent on the infection 4 days after inoculation ($R = -0.44$) (Table 3).

Examination of the degree to which the cuticle penetrates into the deeper skin layers showed that in the varieties Moneymaker, Rutgers, and Robot, it

Table 3

Correlation and multiple regression analysis of anatomical, morphological and infection indicators of tomato fruits

Dependent variable	Optimal multiple regression equation	Test T for $T_{tab.} = 2.02$	Standard error of multiple regression coefficient	Coefficient of partial correlation R for $R_{tab.} = 0.29$	Coefficient of determination R^2	Coefficient of indetermination $1-R^2$	Coefficient of multiple corelation R cal.	Coefficient of multiple corelation R tab.	Number of freedom degrees
Infection after 4 days x_1	$x_1 = 25.19\text{-}0.07\,x_6\text{-}0.07\,x_7$	$T_6 = 5.63$* $T_7 = 2.06$*	$SE_6 = 0.01$ $SE_7 = 0.03$	$R_6 = -0.65$* $R_6 = -0.65$*	0.69	0.31	0.83*	0.37	44
Spot after 14 days x_2	$x_2 = 89.14\text{-}3.21\,x_1{}^0$	$T_{10} = 2.53$*	$SE_{10} = 0.11$	$R_{10} = -0.35$*	0.12	0.88	−0.35*	0.29	45
	$x_2 = 2889 + 103x_1 + 088x_3 + 086x_4$	$T_1 = 1.51$* $T_3 = 1.87$ $T_4 = 2.59$*	$SE_1 = 0.41$ $SE_3 = 0.47$ $SE_4 = 0.33$	$R_1 = 0.36$* $R_3 = 0.27$ $R_4 = 0.37$*	0.29	0.71	0.54*	0.41	43
Fur x_3	$x_3 = \text{-}0.19 + 0.09x_7$	$T_7 = 2.49$*	$SE_7 = 0.03$	$R_7 = 0.35$*	0.12	0.88	0.35*	0.29	45
	$x_3 = 9.09\text{-}0.39x_1 + 0.09x_2\text{-}0.07x_4$	$T_1 = 3.18$* $T_2 = 1.87$ $T_4 = 0.60$	$SE_1 = 0.12$ $SE_3 = 0.05$ $SE_4 = 0.11$	$R_1 = -0.44$* $R_3 = 0.27$ $R_4 = 0.09$	0.21	0.79	0.46*	0.41	43
Fruits streaked with mycelium x_4	$x_4 = 29.59 + 1.33x_{10}$	$T_{10} = 2.61$*	$SE_{10} = 0.51$	$R_{10} = -0.36$*	0.13	0.87	−0.36*	0.29	45
	$x_4 = 9.27 + 0.08x_1 + 0.16x_2\text{-}0.13x_3$	$T_1 = 0.45$ $T_2 = 2.59$* $T_3 = 0.60$	$SE_1 = 0.19$ $SE_2 = 0.06$ $SE_3 = 0.21$	$R_1 = 0.07$ $R_2 = 0.37$* $R_3 = 0.09$	0.19	0.81	0.43*	0.41	43

x_6 – number of hairs
x_7 – covering leyer thickness near calyx
x_{10} – cuticle thickness

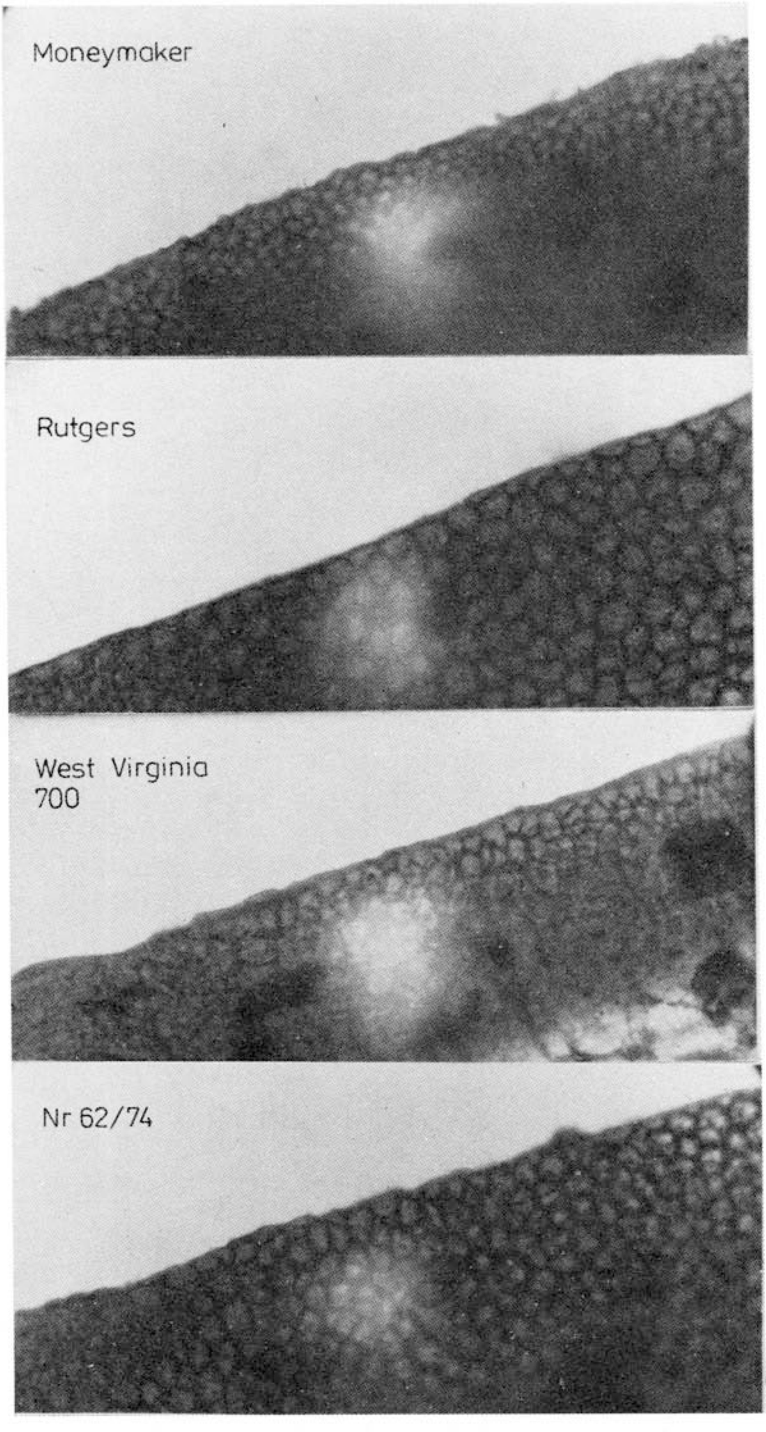
does not penetrate between the epidermis cells, while in the Lines Ottawa 30, No. 155/84 and the species *Lycopersicon hirsutum*, it reaches to the first layer of skin cells. It penetrates the deepest into the skin of fruit from the varieties Szkarłatna Kula and Pieraline which show a certain degree of resistance, although much lower than West Virginia 700. The differences in the cuticle thickness between the susceptible varieties and resistant lines are illustrated on Phots. 1 and 2.

DISCUSSION

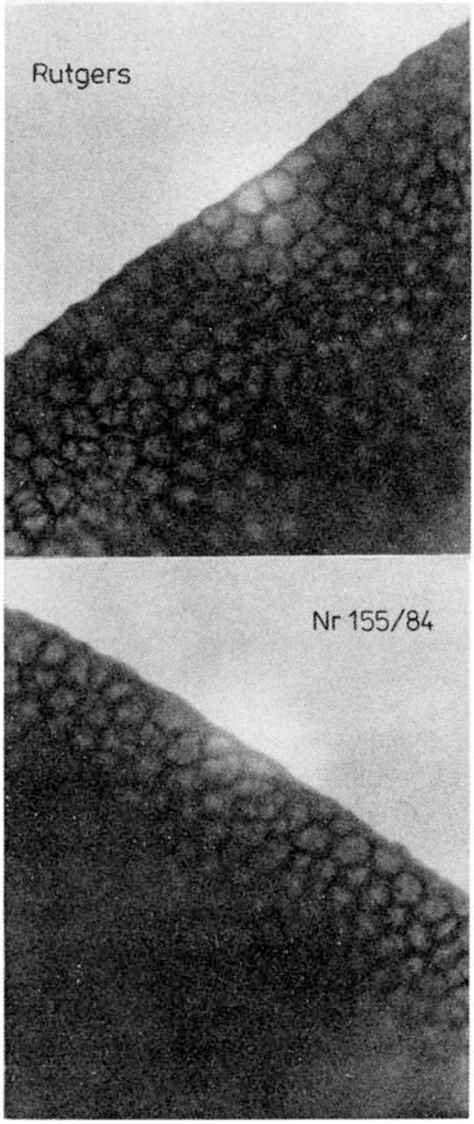
This study was conducted on varieties and breeding lines of tomatoes characterized as resistant, partially resistant and susceptibile and a significant relationship was found between the infection group to which their fruit belonged and some of their anatomical and morphological traits. It was shown that there is a dependence between the extent of infection and the thickness of the covering layer along with the cuticle. The most resistant tomatoes had the thickest skin and cuticle. A similar correlation in respect to the cuticle was observed by Kozhevnikova and Dorozhkina (1971). They found that the average thickness of the cuticle of fruit from susceptible and resistant varieties differed significantly. The cuticle thickness was in their case smaller than in this study, nevertheless, the tendency was similar. The differences may have resulted from differences in the traits of the studied varieties as well as from the fact that cuticle thickness changes with the ripeness of the fruit and is different depending on the part of the tomato from which the pericarp is sampled.

The opposite opinion was voiced by Eggert (1970), who reported that skin thickness plays no part in infection. However, she based these claims on studies conducted on 5 varieties, among which Atom was the most resistant. Under our conditions, the fruit of this variety was susceptible. The present author found that the effect of covering layer thickness on susceptibility depends on the symptom taken as the indicator of infection. For example, initial infection is very much dependent on the covering layer thickness of the fruit near the calycine depression, while the size of the spot after 14 days depends on the cuticle thickness. These symptomos are dependent to a lesser degree or even not at all dependent on the other studied anatomical and morphological traits. Such correlations should be considered taking into account the particular elements of plant resistance, while in order to compare the results with those of other authors, the tests should be conducted under identical conditions.

The resultus obtained in this study point to the existence of structural resistance of the tomato to late blight. It is not the basis of resistance, but surely can play a part in its supplementation. This author has studied the influence of several anatomical and morphological characteristics of the



Phot. 1. Green tomato fruit cuticle. Cross-section of covering layer (magn. 300 ×)



Phot. 2. Green tomato fruit cuticle. Cross-section of covering layer (magn. 300 ×)

tomato on resistance on an extensive range of material, however, resistant varieties and lines made up a relatively small proportion of it. This effect could be studied in more detail if a greater amount of resistant tomatoes were available allowing it to be stated with more certainty if specific anatomical and morphological traits should be the markers for selection.

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Wpływ cech anatomicznych i morfologicznych zielonych owoców pomidora na ich podatność na zarazę ziemniaka (*Phytopthora infestans* (Mont.) de Bary)

Streszczenie

Celem badań przeprowadzonych w latach 1983-1985 było poszukiwanie związków między stopniem podatności zielonych owoców pomidora na zarazę ziemniaka a ich niektórymi cechami anatomicznymi i morfologicznymi. W materiale zróżnicowanym pod względem odporności

stwierdzono, że istnieje zależność porażenia od grubości warstwy okrywającej wraz z kutykulą i od liczby włosków na skórce. Największy wpływ na porażenie po 4 dniach od inokulacji miała liczba włosków i grubość warstwy okrywającej przy kielichu owocu. Na wielkość plamy po 14 dniach od inokulacji i na głębokości przerastania perykarpu grzybnią znaczny wpływ wywierała grubość kutykuli, a na wielkość nalotu grzybni – grubość warstwy okrywającej w dolnej części owocu.

Wyniki te świadczą o odporności strukturalnej pomidorów na zarazę ziemniaka i mogą być pomocne w hodowli odpornościowej.