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IMMUNOLOGICAL ASSESSMENT OF APPLE VARIETIES IN TERMS OF THEIR SCAB RESISTANCE IN RELATION TO LEAF AND FRUIT MICRO STRUCTURE

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(RSAU-MAA named after K A. Timiryazev)

Visual immunological estimation of resistance of apple varieties in Moscow Region to scab causative agent (teleomorph Venturi a inaequalis Aderh., anamorph Fusicladium dendriticum Fuck) and prior attempts of its explanation due to application of methods of scanning electron microscopy studying dependence from micro structural features of leaf and fruits epidermal cover were carried out. Formation of variety-specific micro relief which is changing with age is typical of apple leaves, its elements (cuticle wrinkles near stomata and peristomatic rings) play an important role in resistance to pathogens at the stage of penetration. The possibility of scab causative agent to penetrate not only through cuticle but also through stomatal cracks has been illustrated. Besides, the role of ultra-structural age-related changes in protoplasts of leaf and fruit cells in formation of resistance to phvtopatogenic fungi has been discussed.

Key words: apple tree, resistance, scab, conidia, ultra sculpture, cuticle wrinkles, micro relief, autophagic vacuoles.

In Russia apple plantations occupy approximately 390 thousand hectares and around 2 million tons of apple fruits is harvested annually with average yielding capacity being 5.3 tons per hectare. The yielding capacity and fruit quality are largely dependent on the intensity of apple scab development. Apple scab is known to be among the most malicious diseases of apple trees throughout the entire apple cultivation history. Apple scab is caused by an ascomycete *Venturia inaequalis* Aderh. *(Fusicladium dendriticus* at the conidial stage). To protect apple trees from scab a set of complex effective measures, specific for a particular zone, should be taken. The main techniques used are the following: destruction of affected leaves (serving as the source of infection), chemical methods assuming mostly spraying of vegetating plants by fungicides, growing scab-resistant varieties, etc.

Differences in the varieties' susceptibility to scab are known for a long time. By now many varieties highly resistant or immune to apple scab have been developed all over the world, and Russia is not an exception. These varieties are not affected by scab in the years when the disease is slightly or moderately spread, while in epiphytotic years the harmful effects of apple scab are significantly lower in resistant varieties than in susceptible ones [3]. Amenable varieties require four to six sprayings per season whereas the resistant and moderately resistant cultivars need only three to five sprayings which saves two to three treatments [1,14]. In resistant varieties, the incubation (latent) stage of scab is 1.5 to 2 times shorter compared to susceptible ones [13]. It is well-known that apple scab resistance is regulated by 15 different genes. These genes can be inserted in new varieties by means of traditional breeding methods as well as gene engineering techniques. The achievement of particular genetics make it possible to develop apple varieties with monogenic scab resistance based on Vr gene, identified in a wild apple species *Malus floribnnda* Siebold ex Van Houtte 821. Presently, over 155 apple cultivars with monogenic scab resistance have been developed worldwide.

Among immune varieties developed outside of Russia, such cultivars as Prima, Priscilla, Freedom, Liberty, Sir Prize, Jonafree, Red Free, Priam, Fiorina, Mac Free, Gavin, etc. are known. Domestically bred high-yielding apple varieties immune or highly resistant to scab, according to some authors, are: Imrus, Orlovim, Orlovsky pioneer, Bolotovskoe, Chistotel, Pervinka, Podarok Grafskomu, Yubilyar, Stroyevskoe, Solnyshko, Start, Kandil' orlovsky, Orlovskoe polesie, Prima, etc., as well as small-fruited immune forms of such apple species as *M. floribunda*, *M. ziimi* (Matsum.) Rehder and *M. sctrgentii* Rehder [2, 14]. It is advisable to select scab-resistant varieties with the highest adaptability in terms of ecological, biological and commercially valuable traits. Scab resistance can vary with environmental conditions, stress impact and other factors. The causative agent of apple scab is known for its great variability and adaptive flexibility in response to environmental changes; moreover, natural selection of the pathogen's aggressive forms takes place making the varieties lose their resistance relatively quickly. Therefore, it is essential to have adequate, reliable information about the field resistance and its dynamics in varieties of the modem range and its modifications in the older cultivars.

The causative agent of apple scab can affect plants during almost entire vegetative period provided the temperature and humidity favor the infection. However, there are certain phases of increased vulnerability — in both leaf and fruit development — defined by morphological, anatomical and biochemical peculiarities of these plant parts.

The aim of the present study is to undertake immunological field assessment of the main range of apple varieties at Michurin's orchard of Russian State Agrarian University — MAA named after K.A. Timiryazev in terms of their scab resistance. Another objective is to investigate the structural traits of the epiderm in leaves and fruits at different development stages in both scab-resistant and scab-susceptible cultivars.

Materials and methods

28 new and promising apple varieties in the "young orchard” (trees were planted in 2011) and 10- to 13-year-old apple trees of relatively old varieties were used for a detailed scab assessment. 100 leaves per each experimental tree were examined visually (25 leaves from each of a tree's four sides). The main characteristics taken into account were the development, or progress rate (R) % of the disease and its prevalence rate, or incidence (P) % calculated by means of standard formulas. The intensity of infestation (II) in the studied apple varieties was visually assessed five times per season according to a scale modified by the authors: 0 points — immune variety, no infestation; 1 point — highly resistant, solitary minute spots; 2 points — slightly affected, spots cover up to 10% of the leaf surface; 3 points — moderately affected, spots cover 11-25% of the leaf surface; 4 points — highly susceptible, spots cover over 26% of the leaf surface.

Material was taken from the middle part of crown of three modeled trees. Friuts and leaves were studied directly at maturation and at the stage of maturity. Investigation of miего relief of leaf cover and ultra-sculpture of fruit cover was carried out by means of method of scanning electron microscopy (LE01430 VP, Carl Zeiss, Germany). The samples were placed on freezing console *'Deben CoolStage'* (method CRYOSEM) preliminary covered by thermo paste, cooled to — 30°C and then examined at regimen of high vacuum.

Ultra-structure of leave cells and fruits was investigated by means of transmission electron microscope (JEM-1400).

The method of material preparation for investigations was previously described by the authors in details [8]. Serial ultra thin cross-sections were made by ultra-microtome (LKB-III).

Editing the micro photos and tables was done with CorelDRAW X5 software.

Results and discussion

Weather conditions during the years of research affected the apple plants and the development of fungal diseases in various ways. In general, however, they facilitate only slight and moderate scab development. The first signs of the disease were noticed two to three weeks after complete bud burst. Yellowish spots originally appeared at the upper side of leaves; later on they changed their colour into grayish-black, with dark green velvety coating constituted by conidiophores and conidia and causing further infection spread. Fruits were found to have black spots — minute at first, later they increased in size and fused and were also covered by the velvety coating. Fruit flesh in these areas became suberized, affected fruits ceased the growth, cracked, looked deformed and, if seriously affected, abscised prematurely. Leaf petioles, fruit pedicels, flowers and shoot bark may also suffer from the infection [3].

The materials of our research regarding the degree of scab infestation in leaves and fruits of different apple varieties are given in Table 1.

Our studies show that such new domestically developed varieties as Gulliver, Zvesdochka, Bessemyanka Barantsevoi, Moskovskoe pozdnee, Osennyaya radost', Desertnoe Budagovskogo, Bolotovskoe and Kaluzhanka were not affected by scab during the entire growing season in 2012, while Bogatyr', Spartak, Morozovskoe, Smuglyanka, Borovinka ananasnaya and a clone of Grushyovka moskovskaya demonstrated high scab resistance with the infestation not exceeding 1.5 %. Assessing scab resistance at Kaluga SSTG (state seed-trial ground), S.T. Yesichev [12] has repeatedly proved the resistance of Kaluzhanka and Bolotovskoe cultivars (Vf gene) for 15 years.

Such varieties as Melba, Sinap orlovsky, Rubin, Pamyat' Budakovskogo and Pamyat' voinu appeared to be prone to scab with the progress rate of 6.67% - 11.79% and 100% incidence. Moskovskoe zimnee, Mantet, Sharopai and Zimnyaya krasavitsa had 70 - 80% scab incidence with the progress rate of the infection up to 2.46 - 5.87%. A similar progress rate of the disease was observed in Studencheskoe, Zhigulyovskoe, Pamyat' Michurina, Nakhodka Lebedyanska and Wealthy, however, with lower incidence (50%) — these varieties can also be considered as moderately affected.

The same correlation in terms of varieties' scab resistance was indicated in 2013, though the average progress rate of the disease for most cultivars was by 1.7%-2.5% higher.

The following apple varieties are highly resistant or immune to the scab in middle Russia: Skala, Fregat, Orlovim, Imrus, Pervinka, Kandil orlovsky, Krasulya, Afrodita, Svezhest', Kumakovskoe, Bolotovskoe, Uspenskoe, Chistotel, Start, Blagovest, Solnyshko, Veniaminovskoe, Bylina, Stroevskoe, Yubilyar, Charodeika [8,12]. Out ofthem, Blagovest, T a b l e 1

Results of scab infestation assessment in leaves of apple varieties
(2012, Michurin's orchard of RSAU-MAA, 2-y.o. plants)

N	Variety	II, points	P, %	R, %	N	Variety	II, points	P, %	R, %
1	Melba	1.3	100	8.67	15	Zvesdochka	0	0	0
2	Sinap orlovsky	1.0	100	6.67	16	Zimnyaya krasavitsa	1	80	5.00
3	Bogatyr'	0.4	40	1.07	17	Morozovskoe	0.3	30	0.73
4	Mosк vsкoe zimnee	0.6	70	2.64	18	Wealthy	0.5	50	4.17
5	Spartak	0.2	20	0.27	19	Zhigulyovskoe	0.5	50	2.08
6	Pamyat' Michurina	0.5	50	2.08	20	Bessemyanka Barantsevoi	0	0	0
7	Mantet	1.1	80	5.87	21	Borovinka ananasnaya	0.3	30	1.21
8	Sharopai	0.3	70	2.46	22	Osennyaya radost'	0	0	0
9	Rubin	1.3	100	11.79	23	Grushyovka moskovskaya	0.3	30	1.21
10	Studencheskoe	0.8	50	2.50	24	Mosкovsкoe pozdnee	0	0	0
11	Gulliver	0	0	0	25	Desertnoe Budagovskogo	0	0	0
12	Pamyat' Budakovskogo	1.0	100	6.67	26	Nakhodka Lebedyanska	0.5	50	2.78
13	Pamyat' voinu	1	100	6.67	27	Smuglyanka	0.3	30	1.21
14	Bolotovs кoe	0	0	0	28	Kaluzhanka	0	0	0

Flagman and Fregat are known for their high productivity and monogenic scab resistance and, therefore, are of great economic efficiency. Foreign immune varieties are Gavin, Liberty, Prime, Priscilla, Fiorina, Freedom and Red free.

Most apple varieties possessing Vr and Vf genes still keep their genetic immunity to existing scab races and show no signs of resistance failure under the conditions of middle Russia [8].

Data displayed in Table 2 demonstrate that the leaf scab resistance in apple trees tended to decrease with age and both the incidence and the progress rate of scab appeared to grow.

Table 2

The influence of apple plants age on the scab resistance
(2012, Michurin's orchard of RSAU-MAA)

Variety	2-y.o. plants		10-13-y.o. plants	
	II, points	R, %	II, points	R, %
Zimnyaya krasavitsa	1.0	5.00	1.7	6.25
Orlovsky pioneer	0.0	0.0	1.5	2.66
Bessemyanka Barantsevoi	0.0	0.0	1.5	5.98
Melba	1.3	5.67	2.1	6.68
Sharopai	0.3	2.46	0.9	3.47
Pamyat' voinu	1.0	6.67	1.3	8.79
Wealthy	0.5	4.17	1.0	5.38

Mechanisms of initiation and development of age resistance to scab have not been properly investigated. Application of methods of scanning electron microscopy (SEM) for investigation of leaf and fruit cover of apple during the development allowed the authors to elucidate peculiarities of epidermal organization more deeply and to characterize more folly its functional significance for resistance formation.

Causative agent of apple scab is known to be characterized by the ability to affect plant parts at the period of vegetation, at the certain age and physiological condition, namely young plant tissues and organs.

Primary correspondence of pathogen to affect young tissues of host plant is connected to a mechanism of infecting ectoparasite through unaffected cover tissues. Germinating tubes of spores of pathogen move inside the leaf penetrating epidermis. The hyphae are assumed not to be used for penetration through stomata or mechanical injuries [3].

The last point of view can be opposed, as by means of SEM facts of fungus penetration through stomatal cracks were observed in our investigation many times (fig. 1 A).

When fongal hyphae penetrate the plant tissues not through stomatal cracks but through cuticle exuding enzyme Cutinase which destroys cuticle cover, its structure and character of its sedimentation has an important significance (fig. 1 B).

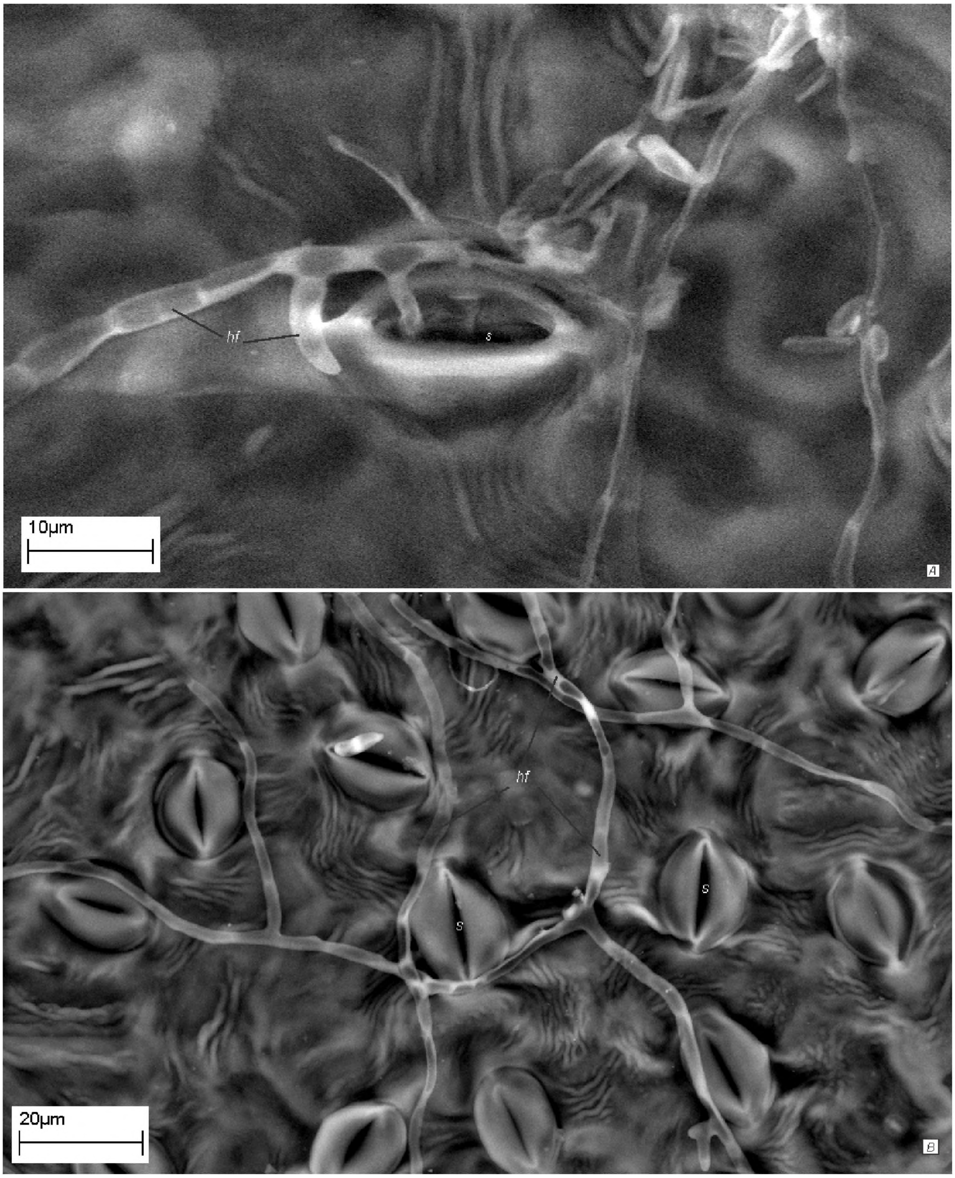

Fig. 1. Fragments of abaxial cover microstructure of apple leaf of Solnishko variety: fungal penetration of hyphae of *V. inaequalis* Aderh. in leaf tissue through *(A)* stoma and (S) cuticle. Designation: *hf*—hyphae; s — stoma

During the growth and development period the leaf apparatus is characterized by age-related and connected structural changes which with a high probability influence the resistance to scab at the stage of pathogen penetration. Character of sedimentation and structure of cuticle and waxen covers contributes to mechanical barrier on the way of pathogenic fungi and bacteria which occur in large amount on plant cover.

Due to water-repellent properties these structures are badly wetted and rolling water droplets clarify plant cover from different pathogens quite effectively and prevent from wet conditions suitable for pathogen development [4, 7]. Thus, fungal development on plant cover and its penetration into internal tissues are hindered, which provides one of the factors of plant resistance to scab causative agent at the stage of penetrating of infective structures.

According to our observations, cuticle of young leaves is thinner (fig. 2 A) than the one on cover of mature leaves (fig. 2 B, C). This proves that leaves of 8-14 days old are the most susceptible organs to scab during ontogenesis, after 10-15 days they became insusceptible [3].

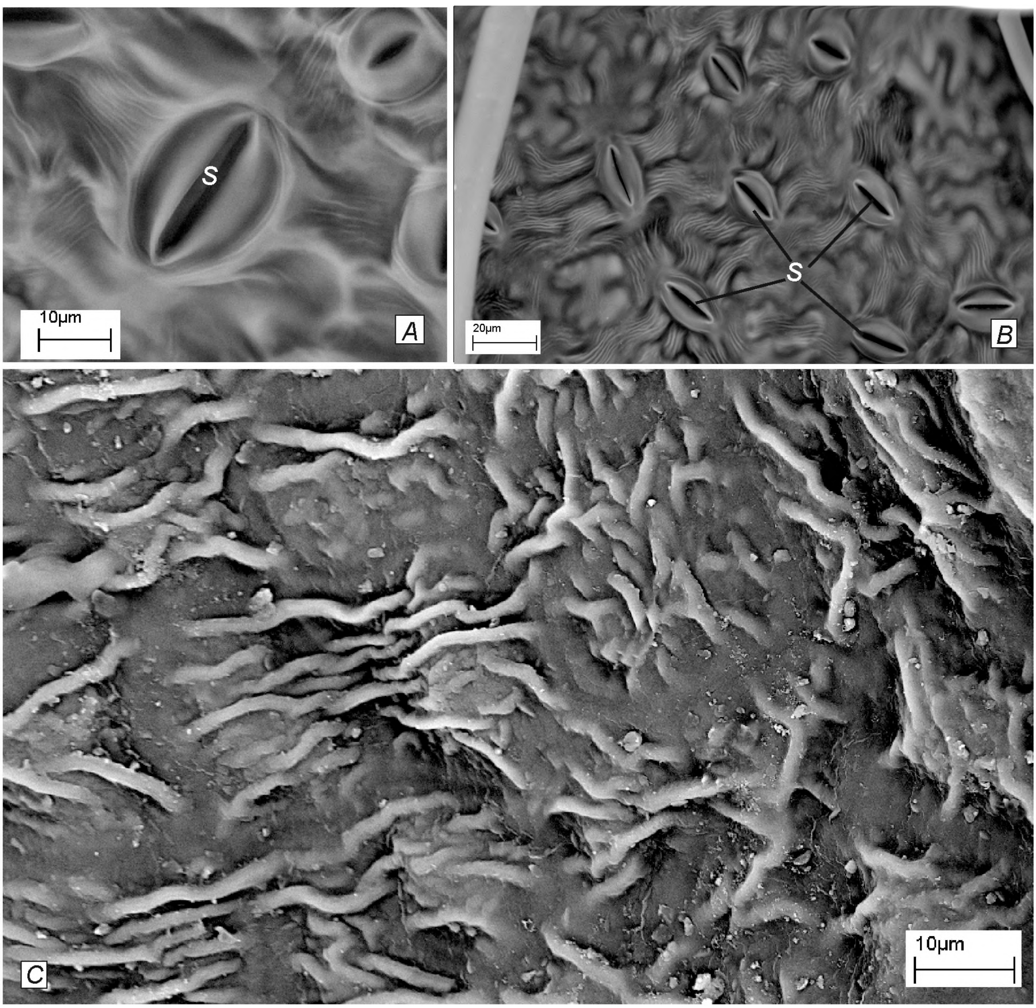

Fig. 2. Fragments of apple leaf microstructure of Solnishko variety: *A* — abaxial cover of young leave (8-10 days); *Б, В* — abaxial and adaxial cover of maturated leave (22-25 days). Designation:
s — stoma

For leaves of the studied apple varieties the original micro relief of epidermal cover was noted (fig. 2). In stomata zone original cuticle wrinkles and peristomatic rings were formed with different intensity. Such cuticle wrinkles significantly decreases wetting ability of leaf cover: water droplets due to high cover tension touch only external margins of cuticle crests and rolled from epidermis [9].

Due to this effect fungal spores which are not tightly attached to cuticle wrinkles are easily washed away. Possibly because of this reason fungal hyphae of

V. inaequalis were detected on leaves of varieties with low leveled resistance to scab and relatively low expressed cuticle wrinkles near stomata.

As it was previously investigated by the authors, fruits differed in their structure and sedimentation type of cuticle and waxen covers (as platters, rods, auriculate form etc.) influencing the penetration rate of fungal pathogens (fig. 3 A, B).

The strongest fruit attack also occurs at initial stages of development (fig. 3 B). In our investigations apple fruits with strongly cutinized and powerful waxen cover were not infected with causative agent of scab (fig. 3 A).

Susceptibility of leaves and fruits to fungal diseases for example to scab can also be caused by synthesis of substances inhibiting pathogen development in cells of cover tissue. Mainly these substances belong to phenols and inhibit germination of fungal conidia [7]. Compounds which suppress spore germination were separated from fruit pericarpium of plants resistant to diseases. Such compounds significantly reducing conidial germination were separated from waxen cover of apple leaves [6, 10].

Besides, inhibitors blocking mycelium development both at the stage of penetration and against already penetrated pathogen are produced in cover tissue cells. In our investigation during the leaf apparatus development stage in mesophyll cells the formation ofbulb like structures was observed, these structures are represented by autophagic vacuoles responsible for particulate utilization of intracellular membranes (fig. 4 A, B). Autophagic vacuoles contain hydrolytic enzymes which under certain conditions move into cytoplasm and initiate its destruction.

More often they appear in differentiating and senescent cells, which was noted in our previous investigations [5]. Intensive formation of phytoalexines — specific protective agents, mainly phenols — is proved to result from the contact with phytopathogenic fungus in plant.

They possess antioxidant properties: restore highly oxidized free radicals, inhibit redox enzymes and suppress formation of active forms of oxygen, which leads to their toxicity for pathogen [9].

It can be supposed that when organelles are destroyed because of intensive cell vacuolization, some compounds toxic for fungus are released, and that results in age ontogenetic resistance of leaves and fruits of apple plants to scab.

Taking Wealthy cultivar as an example, we have also revealed a decrease in field resistance to scab. Earlier, in 1980s - 1990s, it used to be characterized as a variety highly resistant to scab [5], but presently its resistance has substantially decreased, especially in older fruiting plants. The obtained data on the changes in scab resistance of this variety correspond well to I.M. Zueva's research materials [14], who has showed that Wealthy was transferred from the group of slightly affected varieties to the group of moderately affected. Additionally, she points out the tendency of scab resistance to decrease in Zhigulyovskoe, Melba and Vishnyovoe varieties observed in the Central Chernozem Region of Russia. Vishnyovoe, a variety with relatively high scab resistance in the past, is currently close to slightly affected varieties, and Zhigulyovskoe is degraded to the highly susceptible

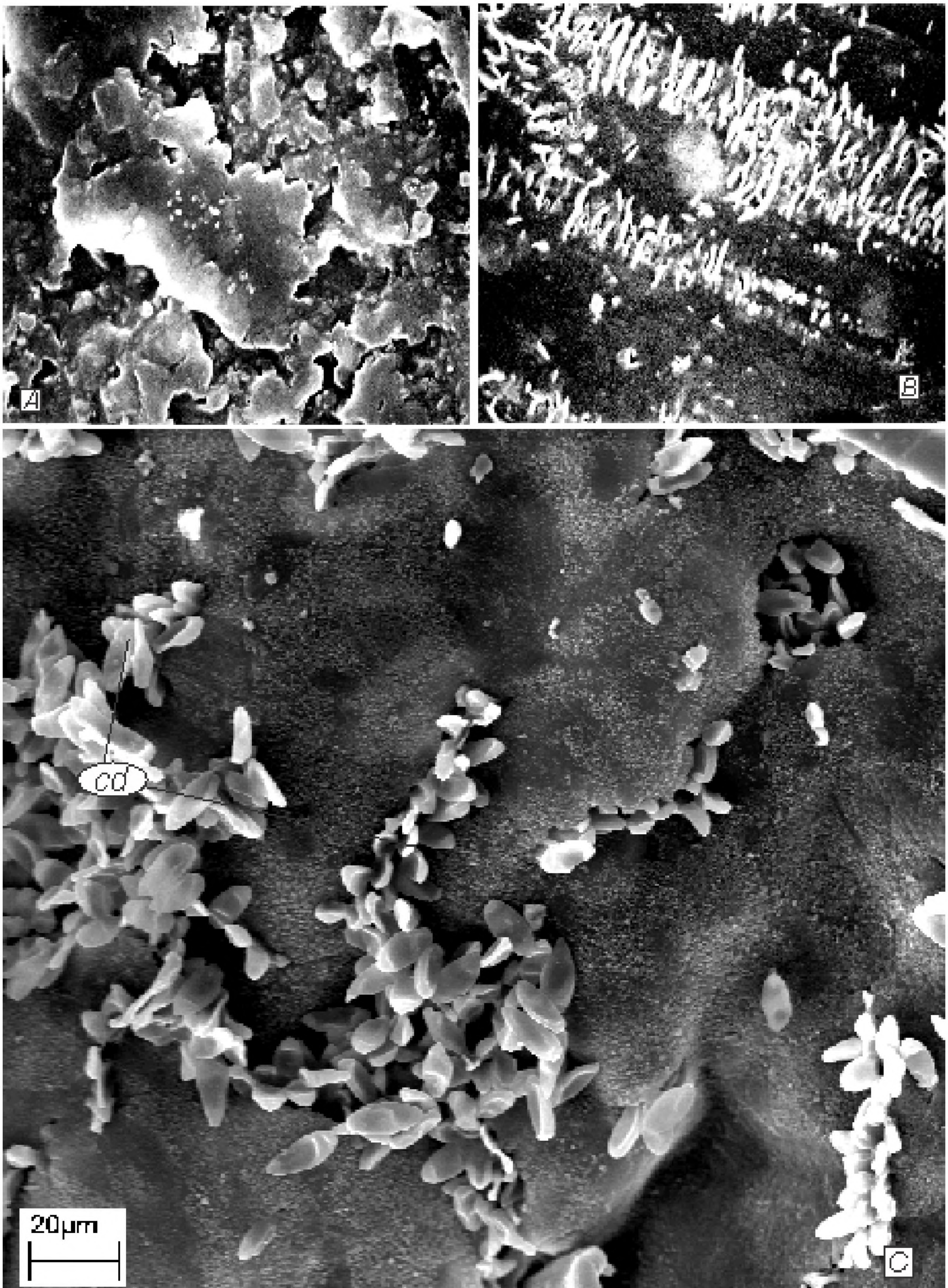

Fig. 3. Apple fruit cover (A) of Solnishko variety and Melba variety (B, C): A — general vision of cover, waxen sediments as platters; B — general vision of cover, waxen sediments as rods; C — part of cover with numerous conidia. Designation: cd — conidia

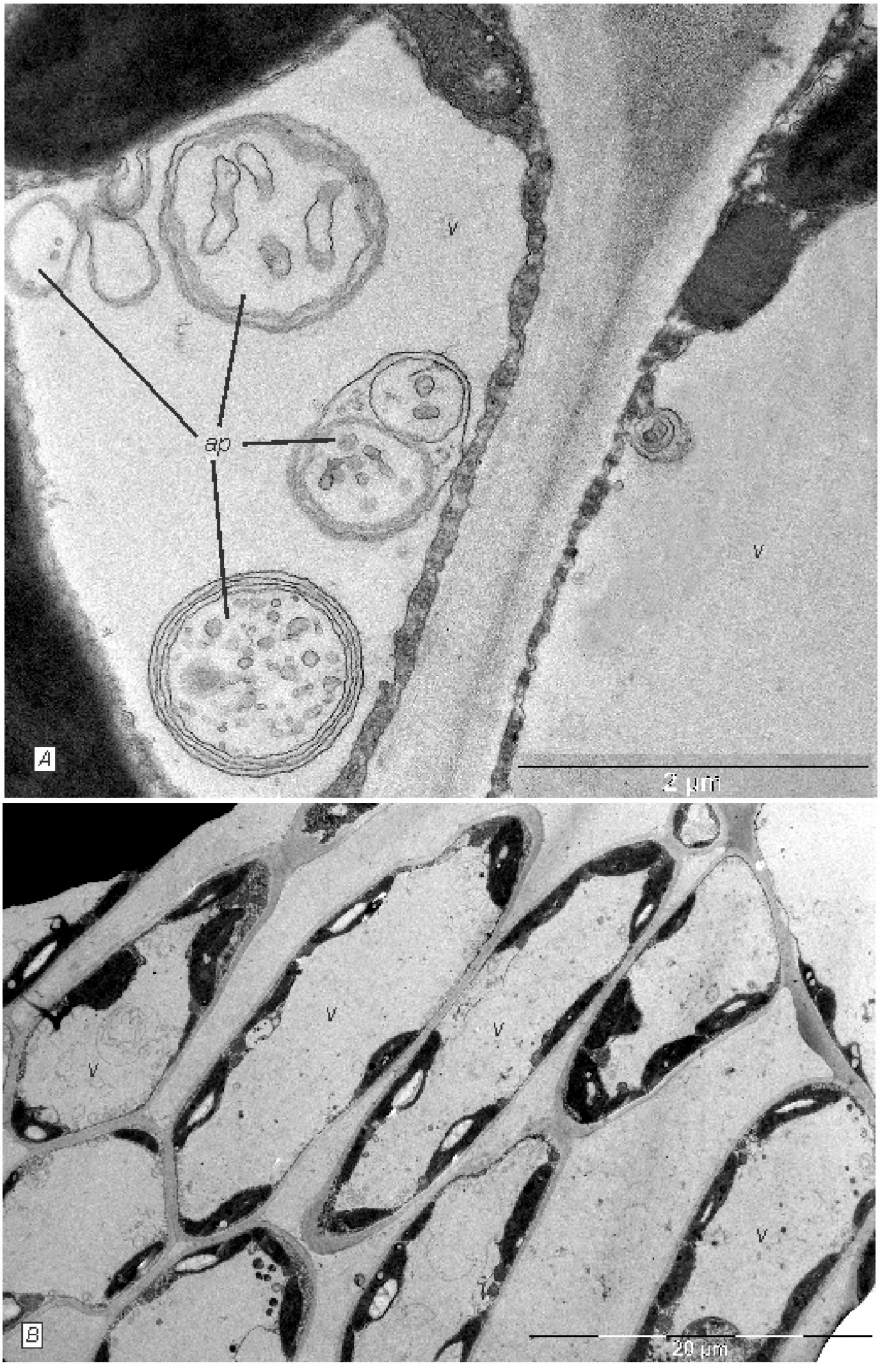

Fig. 4. Fragments of mesophyll cells *(A)* of a young leaf (8-10 days) with autophagic vacuole as membrane whorls and myelin figures and (S) of a matured leaf (22-25 days) of Melba variety. *Designations: ap* — autophagic vacuoles; *v* — vacuole

group. Melba's susceptibility has increased primarily due to higher disease incidence in fruits. The most significant drop in field resistance to apple scab was revealed in the following varieties grown in the southern zone: Borovinka, Belle de Bosque (Boskoop), Noris, Opalescent, Parmen zimnyi zolotoi, Slava pobeditelyam, Suilepskoe, Wealthy and Early Blaze [11].

In conclusion, on the basis of obtained materials and data from relevant literature, the most promising groups of apple varieties as well as those slightly affected by scab and highly susceptible to it, have been identified for Moscow region in Michurin's orchard of RSAU-MAA given as an example. The possibility of penetration of causative agent of scab not only through cuticle but also through stomatal cracks has been illustrated by means of methods of scanning electron microscopy. It can be supposed that scab resistance and other analogical fungal diseases (mycoses) depend on microstructural peculiarities of epidermal cover and ultra-structural age changes of protoplasts of leaf cells and fruits. Our current materials demonstrate advantage of methods of electron microscopy (SEM and TEM) which add to our knowledge about structural organization of apple leaves and fruits, they can also have an important significance for elaboration of measures at fast estimation of apple resistance to negative pathogenic influence.

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ИММУНОЛОГИЧЕСКАЯ ОЦЕНКА УСТОЙЧИВОСТИ К ПАРТТТЕ СОРТОВ ЯБЛОНИ В ЗАВИСИМОСТИ ОТ ОСОБЕННОСТЕЙ МИКРОСТРУКТУРЫ ЭПИДЕРМЫ ЛИСТА И ПЛОДА

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Проведена визуальная иммунологическая оценка к возбудителю парши (телиоморфа Venturi a inaequalis Aderh., анаморфа Fusicladium dendriticum Fuck.) 30 сортов яблони в Мичуринском саду РГАУ-МСХА имени К.А. Тимирязева. Выделены новые сорта отечественной селекции, которые не поражались (8 шт.) или имели слабое поражение (6 шт.) паршой; показано, что с возрастом деревьев возрастала интенсивность их поражения; выявлено снижение полевой устойчивости сорта Уэлси. Сделаны приоритетные попытки объяснения устойчивости с использованием методов электронной микроскопии с точки зрения зависимости от микроструктурных особенностей поверхности эпидермы листьев и плодов. Для листьев яблони отмечено формирование не только сортоспецифического, но и изменяющегося с возрастом микрорельефа, элементы которого (мощность кутикулярных складок в области устьиц и перистоматических колец) влияют на устойчивость к патогенам на этапе их проникновения. Проиллюстрирована возможность проникновения возбудителя парши не только через кутикулу, но и через устьичные щели. Обсуждается роль ультраструктурных возрастных изменений протопласта клеток. В ходе роста и развития листового аппарата в клетках мезофилла формировались автофаговые вакуоли, происходила частичная утилизация внутриклеточных мембран и разрушение органелл, при этом, вероятно, высвобождались токсичные для гриба соединения, что повышало возрастную онтогенетическую устойчивость листьев к парше.

Ключевые слова: яблоня, устойчивость, парша, конидии, ультраскульптура, кутикулярные складки, микрорельеф, автофаговые вакуоли.

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