REVIEW

Case Study of Host-Pathogen Interaction: Tomato (*Lycopersicon* spp.) – Tomato Powdery Mildew (*Oidium lycopersici*)

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Abstract

LEBEDA A., MIESLEROVÁ B. (2000): **Case Study of Host-Pathogen Interaction: Tomato (*Lycopersicon* spp.) – Tomato Powdery Mildew (*Oidium lycopersici*)**. Plant Protec. Sci., **36**: 156–162.

The present paper tries to demonstrate progress and gap of knowledge in plant pathology through the tomato – tomato powdery mildew host-pathogen interaction as a model. Tomato powdery mildew (*Oidium lycopersici*) has caused serious damages on glasshouse tomato (*Lycopersicon esculentum*) crops during the last approximately 15 years. Although the absence of teleomorph stage did not allow exact taxonomic classification of the pathogen, comparative morphological studies using light and scanning electron microscopy revealed that *Oidium lycopersici* might be included to the *Erysiphe* sect. *Erysiphe* (close to *Erysiphe aquilegiae* var. *ranunculi*). Effective resistance sources to *O. lycopersici* were found mainly in wild *Lycopersicon hirsutum* and *L. pennellii* (confirmed by testing with four different *O. lycopersici* isolates). Available information on the pathogenic variability of *O. lycopersici* is given; host range experiments revealed considerable differences in ability of different *O. lycopersici* isolates to infect cucumber and tobacco, postulating existence of different pathotypes /*formae specialis*/ of pathogen. Similarly, some *Lycopersicon* spp. genotypes showed remarkable differential reactions with pathogen isolates, indicating existence of different pathogen races. Information regarding recently detected mechanisms and basis of resistance in *Lycopersicon* spp. are also mentioned. However, more research based on classical, biochemical and molecular approaches is also needed.

Key words: *Lycopersicon* spp.; *Oidium lycopersici*; distribution; taxonomical position; host range; pathogenic variability; resistance sources; basis of resistance; mechanisms of resistance

Recently, phytopathology as a scientific discipline, has become more and more structuralized and specialized. However, in most cases the basic and complex information on pathogenic microorganisms and their interactions with the host plants, has been missing. One of the examples representing this situation is the interaction between tomato (*Lycopersicon* spp.) and tomato powdery mildew (*Oidium lycopersici*). In this paper we want to demonstrate a considerable progress of knowledge on this pathogen during the last decade, but also gaps of basic information important for the better understanding of the host-pathogen interaction.

Geographical Occurrence and Distribution of the Pathogen

Although the first record on the occurrence of tomato powdery mildew (*Oidium lycopersici*) came from Australia in the last century (COOKE & MASSEE 1888), the pathogen has caused serious damages on glasshouse tomato crops during the last approximately 15 years. Firstly causing strong epidemics in the Netherlands in 1986, the pathogen has spread throughout Europe. Informations concerning year of the first occurrence of the pathogen in European countries are shown in Fig. 1. Since 1990s its

*This research was partly supported by the Czech Ministry of Agriculture (Praha) from the "National Programme of Genepool Conservation of Microorganisms and Small Animals of the Economic Importance" and by the project "Stress and Pathological Biology, Biochemistry and Bioenergetics of Plants" (MSM 153100010, Czech Ministry of Education, Youth and Sports, Praha).

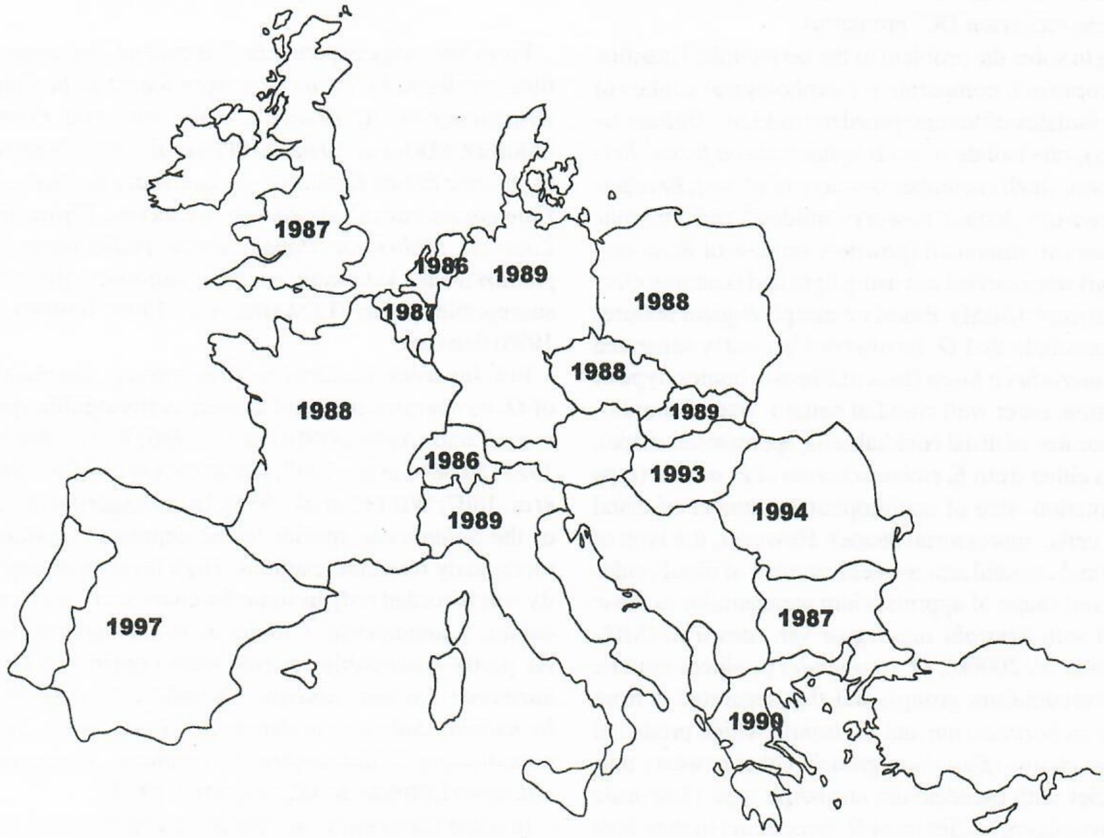

Fig. 1. A map of the first records of *Oidium lycopersici* occurrence in Europe

occurrence has been recorded also in Russia (IGNATOVA *et al.* 1997), India (KUMAR *et al.* 1995) as well as in Canada (BÉLANGER & JARVIS 1994), USA (ARREDONDO *et al.* 1996; KARASEVICZ & ZITTER 1996; SMITH *et al.* 1997; WHITE *et al.* 1997; PERNEZNY & SONODA 1998), Brasil (BOITEUX, 1994) and Venezuela (SANABRIA DE ALBARRACÍN *et al.* 1994)). Nevertheless, the reason of its very fast continental and intercontinental spreading is not known.

In the former Czechoslovakia, *Oidium lycopersici* was recorded on tomato for the first time in 1988 (LEBEDA & ROD 1990). Since that time, regular occurrence of spontaneous infection on leaves of glasshouse-grown tomatoes has been observed in several localities in the Czech Republic (LEBEDA & HALČINOVÁ 1997; LEBEDA *et al.* 1999).

Morphological Characteristics and its Possible Taxonomical Position of *Oidium lycopersici*

Three powdery mildew species have so far been reported on tomato. The first, *Leveillula taurica* (Lév.) Arnaud, 1921 (*Oidiopsis taurica* [Lév.] Salmon) occurs only in warmer regions (PALTI 1988), and is easily distinguished from other powdery mildews by the presence of branched conidiophores growing through the stomata. *Sphaerotheca fusca* (Fr.) Blumer, 1933, emend. Braun, 1995, syn. *Sphaerotheca fuliginea* (Schlecht. ex Fr.) Poll, one of the main powdery mildews of *Cucurbitaceae*, has also been mentioned on tomatoes from the Netherlands (STOLK & COOLS 1983) and Bulgaria (GEORGIEV & ANGELOV 1993). This species is distinguished from other powdery mildews by the presence of fibrosin bodies in conidia. The third species, *Oidium* spp. (including *O. lycopersici*) is a different species both morphologically and biologically. Until now, no teleomorph stage of *O. lycopersici*, has been found thus the taxonomical position of this pathogen is still unclear (MIESLEROVÁ & LEBEDA 1999a). Moreover, the attempt to initiate formation of cleistothecia under laboratory conditions using different isolates of *O. lycopersici* under various temperature conditions, has failed (MIESLEROVÁ & LEBEDA, unpubl.).

However, on the base of morphological characteristics of its anamorphic stage (shape of conidia, conidiophores and absence of fibrosin bodies), the pathogen was referred as possibly belonging to genus *Erysiphe* (FLETCHER *et al.* 1988, KISS *et al.* 1999). The fact, that *O. lycopersici* can also infect cucurbitaceous species (FLETCHER *et al.* 1988; CORBAZ 1993; LEBEDA & MIESLEROVÁ 1999) and that the occurrence of *Erysiphe orontii* on *Solanaceae* was confirmed (HAMMARLUND 1945; BRAUN 1987, 1995), suggested that *O. lycopersici* may be related to

Erysiphe orontii Cast. 1851 emend. Braun, 1987 (= *Erysiphe cichoracearum* DC. pro parte).

Trying to solve the problem of the taxonomical position of *O. lycopersici*, comparative morphological studies of fourteen isolates of tomato powdery mildew (*Oidium lycopersici*), one isolate of each *Sphaerotheca fusca, Erysiphe orontii* (both cucumber powdery mildews), *Erysiphe cichoracearum* (lettuce powdery mildew) and *Erysiphe aquilegiae* var. *ranunculi* (powdery mildew of *Ranunculus lingua*) were carried out using light and scanning electron microcopy (SEM). Based on morphological features we can conclude that *O. lycopersici* is clearly separated from *Sphaerotheca fusca* (lack of fibrosin bodies, type of germination, outer wall conidial pattern, size of conidiophores, number of distal conidial cells, appressorial shape), as well as either from *E. cichoracearum* or *E. orontii* (type of germination, size of conidiophores, number of distal conidial cells, appressorial shape). However, the type of germination, conidial arrangement, number of distal conidial cells and shape of appressorium were similar to those observed with *Erysiphe aquilegiae* var. *ranunculi* (MIESLEROVÁ *et al.* 2000b). *O. lycopersici* produces conidia singly (Pseudoidium group), and this separated it from *Erysiphe cichoracearum* and *E. orontii*, which produced conidia in chains (*Euoidium* group). Other powdery mildew species with pseudoidium anamorph type (*Uncinula* and *Microsphaera*) differ from *O. lycopersici* in their host range, suggesting a closer relationship of *O. lycopersici* to *Erysiphe* sect. *Erysiphe* (BRAUN 1995; COOK *et al.* 1998), and to *Erysiphe aquilegiae* var. *ranunculi* (Fig. 2).

Nevertheless, to solve clearly the taxonomical position of *O. lycopersici*, more research based on classical and molecular approaches is required.

Host Range of the Pathogen

From host range experiments it is evident, that no susceptible species to *O. lycopersici* were found in the families *Brassicaceae*, *Asteraceae*, *Fabaceae* and *Poaceae* (ARREDONDO *et al.* 1996; WHIPPS *et al.* 1998). Surprisingly, in some distant families, e.g. *Apocynaceae, Asteraceae, Campanulaceae, Crassulaceae, Cistaceae, Dipsacaceae, Linaceae, Malvaceae, Papaveraceae, Pedaliaceae, Scrophulariaceae, Valerianaceae* and *Violaceae*, there were susceptible species (LEMAIRE *et al.* 1999; WHIPPS *et al.* 1998) detected.

In *Solanaceae*, besides *Lycopersicon* spp., the main host of *O. lycopersici*, resistant as well as susceptible species were found (ARREDONDO *et al.* 1996; FLETCHER *et al.* 1988; HUANG *et al.*, 1997; IGNATOVA *et al.* 1997; SMITH *et al.* 1997; WHIPPS *et al.* 1998). In our experiments, most of the *Solanaceae* species tested expressed resistant or moderately resistant reactions. High level of susceptibility was recorded only in some *Solanum* species (*S. capsicoides, S. jamaicense, S. laciniatum, S. lycopersicoides*). As partly susceptible species were considered *Lycium barbatum, Lycium chinense, Physalis alkekengi, Physalis minima, Solanum aethiopicum, S. aviculare, S. chenopodioides, S. dulcamara, S. incanum, S. nigrum, S. villosum* (LEBEDA & MIESLEROVÁ 1999).

In some *Cucurbitaceae* species (*Cucumis melo, C. sativus, Cucurbita* spp.) the development of powdery mildew symptoms and sporulation were recorded, and only *Citrullus lanatus* could be considered as resistant or moderately susceptible (LEBEDA & MIESLEROVÁ 1999). Interestingly, the most controversial results are related to the ability of different *O. lycopersici* isolates to infect both cucumber and tobacco (CORBAZ 1993; FLETCHER *et al.*

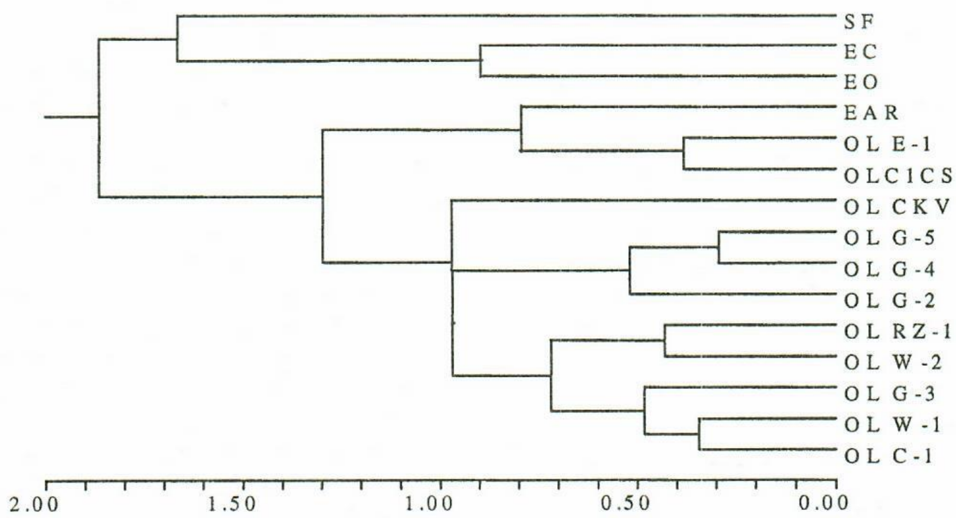

Fig. 2. Dendrogram constructed on the basis of morphological data (length, width and shape index of conidia; presence of fibrosin bodies; length of conidiophores; length and width of conidiophore foot-cell; the number of distal conidial cells; germination type and appressorium shape) of *O. lycopersici* (OL), *Erysiphe aquilegiae* var. *ranunculi* (EAR), *E. cichoracearum* (EC), *E. orontii* (EO) and *Sphaerotheca fusca* (SF) showing similarity between isolates (according to MIESLEROVÁ *et al.* 2000b)

Table 1. Records on the ability of different *Oidium lycopersici* isolates to infect some plant species

Origin	Report	*Cucumis sativus*	*Nicotiana tabacum*	*Solanum melongena*
CZ	LEBEDA & MIESLEROVÁ (1998)	+	–	–
F	LEMAIRE *et al.* (1999)	+	+	+
HU	KISS (1996)	–	–	nd
CH	CORBAZ (1993)	+	+	nd
NL	HUANG *et al.* (1998a, b)	–	+	+
RUS	IGNATOVA *et al.* (1997)	+	+	nd
UK	FLETCHER *et al.* (1988)	–	+	+
UK	WHIPPS *et al.* (1998)	+	+	+
USA	LAMONDIA *et al.* (1999)	nd	+	+

+ susceptible; – resistant; nd – not determined

1988; IGNATOVA *et al.* 1997; WHIPPS *et al.* 1998). Thus, some authors confirmed successful transfer of tomato powdery mildew onto cucumber and tobacco, while others did not (Table 1). These results suggest that cucumber and tobacco may be potentially used for differentiation of *O. lycopersici* pathotypes.

From the experimental data mentioned above it is evident that there is a lot of confusion regarding host range of *O. lycopersici* which must be solved.

Sources of Resistance against *O. lycopersici* among Wild *Lycopersicon* Species

Some recent results showed that nearly all cultivars of *Lycopersicon esculentum* released till 1990s were highly susceptible to *O. lycopersici* (KOZIK 1993; LINDHOUT *et al.* 1994a), nevertheless there were differences in the level of susceptibility (LEMAIRE *et al.* 1999). Therefore, the screening of wild *Lycopersicon* spp. as a potential resistance sources was initiated. So far, the most valuable donors of resistance have been found in *L. hirsutum*, *L. chilense*, *L. parviflorum*, *L. peruvianum* and *L. pennellii* (IGNATOVA *et al.* 1997; LINDHOUT *et al.* 1994a; MILOTAY & DORMANNS-SIMON 1997), and this was also confirmed in our experiments (MIESLEROVÁ & LEBEDA 1998; MIESLEROVÁ *et al.* 2000a). However, *L. esculentum* (*L. esc.* var. *cerasiforme*, *L. esc.* var. *piriforme*) and *L. pimpinellifolium* (the closest relatives of cultivated tomato) generally expressed high susceptibility to *O. lycopersici* (CICCARESE *et al.* 1998; KUMAR *et al.* 1995; MIESLEROVÁ & LEBEDA 1998; MIESLEROVÁ *et al.* 2000a). The results obtained well coincide with RFLPs that showed genetic distance among populations and species of the genus *Lycopersicon* (MILLER & TANKSLEY 1990).

More detailed research is urgently needed on the variability of resistance, first of all from the viewpoint of pathogenicity differences to *O. lycopersici*.

Pathogenic Variability of *Oidium lycopersici*

Limited information is available on pathogenic variability of *O. lycopersici*. Although host range studies revealed considerable differences, mainly in the ability of various *O. lycopersici* isolates to infect representatives of the *Cucurbitaceae* family, postulating the existence of different pathotypes [*formae specialis*] of the pathogen (HUANG *et al.* 1998b; MIESLEROVÁ & LEBEDA 1999a).

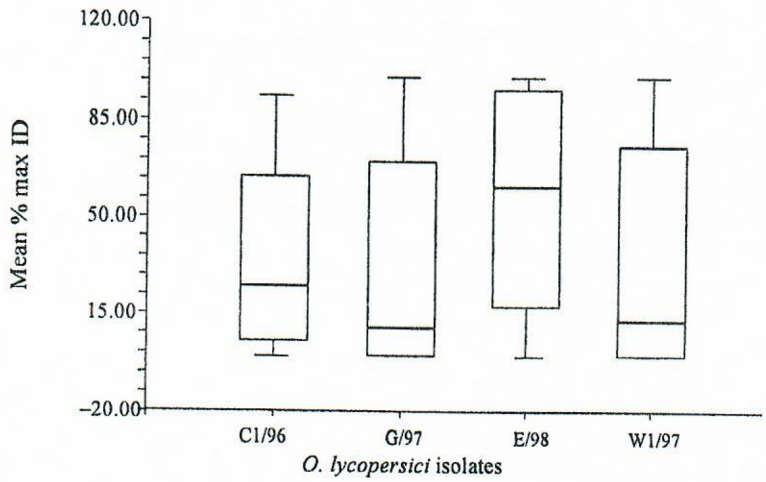

Fig. 3. Comparison of four *O. lycopersici* isolates originating from the Czech Republic (C1/96), Germany (G/97), the Netherlands (W1/97) and England (E/98) based on % max ID values obtained after inoculation with 35 *Lycopersicon* spp. genotypes

However, till now no scientific work was aimed to study the pathogenic variability of *O. lycopersici* at race specialization level (differences in responses of several genotypes of one species and/or related species). This is probably because nearly all recent tomato cultivars are considered as highly susceptible, and thus not possible for differentiation of *O. lycopersici* isolates. In the Netherlands, the application of AFLP markers allowed to differentiate four *O. lycopersici* isolates (HUANG *et al.* 1998b) and the results revealed at least two different patterns related to two types of *O. lycopersici* isolates existing in the Netherlands. However, level of pathogenicity was not assessed in this case.

In our recent experiments, the pathogenicity of *O. lycopersici* isolates originating from the Czech Republic, Germany, the Netherlands and England were compared using data (percentage of maximal infection degree (% max ID) from inoculation experiments on 35 (resp. 60) accessions of wild *Lycopersicon* species. The Fig. 3. showed large variability within the tested isolates. The English isolate of *O. lycopersici* was found to have specific and high pathogenicity (Fig. 3). In other experiments, the value of some germplasm of wild *Lycopersicon* spp. as a resistance sources (*L. hirsutum, L. pennellii*) was confirmed. Some *Lycopersicon* spp. genotypes, which showed remarkable differential reactions with pathogen isolates, were proposed as members of a preliminary differential set (Table 2).

Table 2. A list of *Lycopersicon* spp. accessions recommended for use in a preliminary differential set

Lycopersicon spp.	Accession	*O. lycopersici* isolate/response			
		C1/96	G/97	W1/97	E/98
L. esculentum	cv. Amateur	S	S	S	S
L. hirsutum	LA 94	S	S	R	M
L. hirsutum	LA 1738	R	R	R	S
L. hirsutum	LA 1731	R	R	R	M
L. hirsutum f. *glabratum*	LA 2128	R	R	R	R

R – resistant ; M – moderately susceptible; S – susceptible

Nevertheless, to perform a more exact determination of these interactions we will need more experimental data at population, individual, biochemical and molecular level.

Genetic Basis of Resistance

Only few experiments tried to study the genetic background of resistance to *O. lycopersici* in wild *Lycopersicon* spp. It was suggested that monogenic incompletely dominant genes, recessive genes, and even polygenes could be responsible for resistance (BEEK *et al.* 1994; CICARESSE *et al.* 1998; HUANG *et al.* 1998a; LINDHOUT *et al.* 1994b; MIESLEROVÁ & LEBEDA 1999a). In our experiments only a few of tested *Lycopersicon* spp. genotypes matched typical race-specific resistance, which was characterized by nearly complete resistant reaction to three of the tested *O. lycopersici* isolates and, by high susceptibility to the English isolate. In most cases results evoked the presumption that resistance is of quantitative type (no absolute resistance) controlled by polygenes. In fact, the experiences mentioned above suggest that this pathosystem could be controlled by a gene-complex, including polygenes together with major genes.

Further more classical and molecular genetic research is required to get more detailed information on this host-pathogen genetics.

Resistance Mechanisms in *Lycopersicon* spp. to *O. lycopersici*

Only limited information is still available on the resistance mechanism in *Lycopersicon* spp. – *Oidium lycopersici* interaction. LINDHOUT *et al.* (1994a) described that resistance to *O. lycopersici* in wild *Lycopersicon* species is macroscopically characterized by a very low amount of infection, a strongly restricted mycelial growth and lack of sporulation. Histological studies of the resistance mechanism in plants infected by *O. lycopersici* were reported by HUANG *et al.* (1997, 1998a). They found that prevailing, but often not completely effective resistance mechanism occurred in *Lycopersicon* spp. as a hypersensitive (necrotic) response.

For studying the infection process of *O. lycopersici*, histological and biochemical research (changes in activities of peroxidase and catalase) were carried out in ten *Lycopersicon* spp. genotypes (including wild *Lycopersicon* spp. and two "oidium resistant" tomato lines). The experiments showed that plant genotype did not efficiently inhibited conidium germination. However, in early stages of *O. lycopersici* infections significant differences in germ tube development were recorded in resistant and susceptible accessions. The main resistant reaction detected was hypersensitive (necrotic) response, which was, however, often followed by pathogen development. In addition, the existence of different resistant mechanisms not based on hypersensitivity were confirmed as well. Increased peroxidase activity during pathogenesis was detected mainly in moderately resistant accessions and closely correlated with the occurrence of cell necrosis (hypersensitivity). Because of the fact, that catalase can be considered as a substrate competitor of peroxidase, increasing in their activity was detected in highly resistant accessions, in which the peroxidase changes and the occurrence of hypersensitivity were limited (LEBEDA *et al.* 1999; MIESLEROVÁ & LEBEDA 1999b).

Future Prospects

Present survey has shown that our knowledge on the interaction *Lycopersicon* spp. – *O. lycopersici* is still limited. The intraspecific variation of *O. lycopersici* and the genetics of host-pathogen system represents "gap of knowledge" from the viewpoint of both theoretical and practical aspects. Sufficient amount of specified plant material and further investigations with a range of different and well-specified *O. lycopersici* isolates (races) could help in better understanding of these interactions. Furthermore, detailed characterization of resistance background in the host germplasm can improve their effectivenes as sources of resistance suitable for incorporating into tomato cultivars.

Acknowledgements: The authors acknowledge the fruitful remarks of Prof. Dr. F. VIRÁNYI to the earlier draft of the manuscript.

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Souhrn

LEBEDA A., MIESLEROVÁ B. (2000): **Studium interakce hostitel – patogen: rajče** (*Lycopersicon* spp.) **– padlí rajčat** (*Oidium lycopersici*). Plant Protect. Sci., **36**: 156–162.

Fytopatologie se v posledních letech stává stále více strukturovanou a specializovanou vědeckou disciplínou, a to i přesto, že v řadě případů postrádáme základní informace o patogenních mikroorganismech a jejich interakci s hostitelskou rostlinou. Jedním z příkladů této situace může být i interakce rajče (*Lycopersicon* spp.) – padlí rajčat (*Oidium lycopersici*). Právě u tohoto patosystému lze demonstrovat určitý pokrok poznání, který nastal ve fytopatologii v průběhu posledních let. Padlí rajčat (*Oidium lycopersici*) způsobuje v posledních přibližně patnácti letech vážné škody na skleníkových porostech rajčat (*Lycopersicon esculentum*). Ačkoliv doposud nebylo nalezeno pohlavní stadium patogena, srovnávací morfologické studium nepohlavních stadií padlí (světelnou a elektronovou mikroskopií) prokázalo, že *Oidium lycopersici* může být zařazeno do rodu *Erysiphe* sect. *Erysiphe* (blízko *Erysiphe aquilegiae* var. *ranunculi*). Významné zdroje rezistence byly nalezeny hlavně mezi genotypy druhů *Lycopersicon hirsutum* and *L. pennellii* (což bylo potvrzeno testováním více izoláty *O. lycopersici*). V předloženém příspěvku jsou také shrnuty poznatky o intraspecifické variabilitě patogena. Z výsledků studia hostitelského okruhu vyplývá, že existují značné rozdíly ve schopnosti různých izolátů *O. lycopersici* infikovat např. okurku (*Cucumis sativus*) a tabák (*Nicotiana tabacum*), což poukazuje na potenciální existenci různých patotypů /*formae specialis*/ patogena. Podobně byly zjištěny rozdílné reakce některých genotypů rodu *Lycopersicon* vůči různým izolátům *O. lycopersici*, což potvrzuje existenci různých ras patogena. Příspěvek podává také informace o mechanismech rezistence a pravděpodobném genetickém založení rezistence. Závěrem je nutné podotknout, že je potřeba dalšího intenzivního komplexního výzkumu patogena za použití nejnovějších molekulárních, ale i klasických metod.

Klíčová slova: *Lycopersicon* spp.; *Oidium lycopersici*; rozšíření; taxonomická pozice; okruh hostitelů; variabilita patogenů; zdroje rezistence; mechanismus rezistence; založení rezistence

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