TOMATO POWDERY MILDEW – A NEW DANGEROUS DISEASE IN EUROPE

Aleš LEBEDA[1], Barbora MIESLEROVÁ[2]
Palacký University, Faculty of Science, Department of Botany

ABSTRACT

Tomato powdery mildew (Oidium lycopersici) has attracted the attention of plant pathologists and breeders for more than 10 years, since it started to cause epidemics on tomato. It is dangerous pathogen which spreaded through temperate areas in the Old and New Worlds, and which origin is not exactly known (probably mutation of unknown species). Till now the experimental studies were concentrated mainly on morphological characterization of this pathogen, host range and searching for resistance sources within genus *Lycopersicon* (including study of defence mechanisms and basis of resistance). However, less data is available on biology of this pathogen and its intraspecific variation. Authors in their contribution summarized recent information on this pathogen, with emphasis on their own experimental data.
In survey are enlighted problems of pathogen identification, because absence of teleomorph stage did not allow its exact taxonomic classification. Recent studies, including comparative morphological observations and genetical analysis, show that *O. lycopersici* can be referred to *Erysiphe* sect. *Erysiphe* and it is nearly identical to *Erysiphe aquilegiae* var. *ranunculi*. Screening of wild *Lycopersicon* spp. for resistance to *O. lycopersici* revealed valuable sources of resistance, mainly among *L. hirsutum* and *L. pennellii* (confirmed by testing with four different *O. lycopersici* isolates), opposite to high susceptibility recorded in *L. esculentum* var. *cerasiforme* and *L. pimpinellifolium*. Host range studies, besides detecting of some alternative hosts of *Oidium lycopersici*, showed high intraspecific variability on the level of pathotypes (*formae speciales*). Other studies confirmed that *O. lycopersici* isolates may also differ in pathogenicity within one plant genus and/or species. Among *Lycopersicon esculentum* cultivars and lines there was not found significant variation for resistance to *O. lycopersici*, because of their high susceptibility. However, authors give the first clear evidence about phenomenon of race-specificity in interaction wild *Lycopersicon* spp. - *O. lycopersici* and existence of tomato powdery mildew races. Information regarding recently detected mechanisms and basis of resistance in *Lycopersicon* spp. is also mentioned. However, more research based on classical, biochemical and molecular approaches is needed.
Key words: *Lycopersicon* spp., *Oidium lycopersici*, taxonomical position, host range, resistance sources, pathogenic variability, mechanisms of resistance

[1,2] dr., Palacký University, Faculty of Science, Department of Botany, Šlechtitelů 11, 783 71 Olomouc-Holice, Czech Republic, e-mail: lebeda@prfholnt.upol.cz

IZVLEČEK

PARADIŽNIKOVA PEPELOVKA – NOVA NEVARNA BOLEZEN V EVROPI

Paradižnikova pepelovka (Oidium lycopersici) je pritegnila pozornost fitopatologov in žlahniteljev že pred več kot 10 leti, ko je prišlo zaradi nje do epifitocije na paradižniku. Gliva je nevaren patogen in se je razširila v zmerno toplem območju starega in novega Sveta. Njen izvor ni natančno znan (verjetno pa gre za mutacijo neznane vrste). Doslej so bile raziskave usmerjene predvsem k morfološkim značilnostim glive, vrstam gojiteljskih rastlin in k izvoru odpornosti znotraj rodu *Lycopersicum* (vključujoč raziskave obrambnih mehanizmov osnov odpornosti). Vendar pa je dosegljivo malo podatkov o biologiji patogena in o znotrajvrstnih razlikah. V tem prispevku predstavljamo novejše podatke o patogenu s poudarkom na lastnih raziskavah. V prispevku je osvetljena problematika identifikacije patogena. Zaradi odsotnosti teleomorfnega stadija je bila otežkočena natančna taksonomska uvrstitev glive. Zadnje raziskave, ki vključujejo primerjalna morfološka opazovanja in genetske analize, kažejo na to, da je mogoče *O. lycopersici* uvrstiti v *Erysiphe* sect. *Erysiphe* in da je skoraj identična z *Erysiphe aquilegiae* var. *ranunculi*. Iskanja divjih vrst *Lycopersicon*, odpornih za *O. lycopersici*, so razkrila dragocene izvire odpornosti, večinoma med *L. hirsutum* in *L. pennellii* (kar so potrdila testiranja s štirimi različnimi izolati *O. lycopersici*). Ugotovljena pa je bila tudi velika občutljivost za *L. esculentum* var. *cerasiforme* in *L. pimpinellifolium*. V okviru raziskav gostiteljev smo razen alternativnih gostiteljev za *Oidium lycopersici* ugotovili visoko stopnjo variabilnosti glede patotipov *(formae specialis)*. Druge raziskave pa so pokazale, da so izolati vrste *O. lycopersici* različno patogeni za gostiteljske rodove in/ali vrste. Med kultivarji in linijami *Lycopersicum aesculentum* niso našli signifikantnih razlik v odpornosti za *O. lycopersici* zaradi njegove velike občutljivosti. V prispevku navajamo prve jasne dokaze za pojav rasne specifičnosti v interakcijah divjih *Lycopersicum* vrst – *O. lycopersici* in za obstoj ras pri glivi *O. lycopersici*. Navajamo tudi mehanizme in podlage za odpornost pri *Lycopersicum* spp. V bodoče bo potrebno pospešiti tovrstne raziskave s klasičnimi, biokemijskimi in molekulskimi metodami.

Ključne besede: *Lycopersicon* spp., *Oidium lycopersici,* taksonomski položaj, gostiteljske rastline, viri odpornosti, variabilnost patogenosti, mehanizem odpornosti

1. INTRODUCTION

Tomato powdery mildew (*Oidium lycopersici*) has attracted the attention of plant pathologist and breeders for more than 10 years, since it started to cause epidemics on tomato (Mieslerová and Lebeda, 1999a). It is dangerous pathogen which spreaded through temperate areas in the Old and New Worlds, and which origin is not exactly known (probably mutation of unknown species). Till now the experimental studies were concentrated mainly on morphological characterization of this pathogen, host range and searching for resistance sources within genus *Lycopersicon* (including study of defence mechanisms and basis of resistance). However, less data is available on the biology of this pathogen and its intraspecific variation. Authors in their contribution summarize recent information on this pathogen, with emphasis on their own experimental data.

2. TAXONOMICAL POSITION OF *O. LYCOPERSICI*

In this part authors try to enlight problems of pathogen identification, because absence of teleomorph stage did not allow its exact taxonomic classification (Whipps *et al.*, 1998). The origin of the pathogen is discutable. It is evident that *O. lycopersici* is different from all powdery mildew species previously recorded on tomato. In our comparative morphological studies fourteen isolates of tomato powdery mildew (*Oidium lycopersici*) and one isolate of *Sphaerotheca fusca, Erysiphe orontii* (cucumber powdery mildews), *Erysiphe cichoracearum* (lettuce powdery mildew) and *Erysiphe aquilegiae* var. *ranunculi* (*Ranunculus lingua* powdery mildew) were used. Basic anamorphic characteristics including outer conidial wall patterns were compared using light and scanning electron microscopy (SEM) (Cook *et al.*, 1998). In main morphological features, *O. lycopersici* was strongly differentiated from *E. cichoracearum, E. orontii* and *S. fusca*. However, based on morphological features, (e. g. germination type; appressorium shape; morphology of conidiophores) *O. lycopersici* was close to *E. aquilegiae* var. *ranunculi* (both belong to *Oidium* subgen. *Pseudooidium*) and it probably could be placed to *Erysiphe* sect. *Erysiphe* (= *Erysiphe* s. str.) (Lebeda and Mieslerová, 2000a).
The similar results were obtained by Jones *et al.* (2000). They compared the rDNA intergenic spacer sequence of *O. lycopersici* with the sequences of other powdery mildew species. From their study, *O. lycopersici* is essentially identical to *E. aquilegiae* var. *ranunculi,* and is clearly distinct from *E. cichoracearum* and *E. orontii.* In agreement with these results, Takamatsu *et al.* (1998) in their work using ITS sequence analysis clearly separates *E. aquilegiae* from *E. cichoracearum.*
Although present morphological and genetical studies confirmed similarities between *O. lycopersici* and *E. aquilegiae* var. *ranunculi,* the transfer of *E. aquilegiae* var. *ranunculi* from *Ranunculus lingua* and *Ranunculus repens* to the *L. esculentum* was not successful (Mieslerová and Lebeda, unpubl.). Thus, the importance and value of these approaches (molecular, biological and morphological) in taxonomy and plant pathology must be seriously considered.

3. HOST RANGE OF *O. LYCOPERSICI*

Results of our host range studies (including 70 representatives of Solanaceae and 7 from Cucurbitaceae and Czech *O. lycopersici* isolate) revealed high level of susceptibility only in some *Solanum* species (*S. capsicoides, S. jamaicense, S. laciniatum, S. lycopersicoides*). As a partly susceptible species could be considered *Lycium barbatum, Lycium chinense, Physalis alkekengi, Physalis minima, Solanum aethiopicum, S. aviculare, S. chenopodioides, S. dulcamara, S. incanum, S. nigrum, S. villosum.* Also some Cucurbitaceae (*Cucumis melo, C. sativus, Cucurbita* spp.) were found to be highly susceptible to *O. lycopersici* (Lebeda and Mieslerová, 1999a).
Some of these results are in accordance with other studies, in some cases others give different results, mainly regarding pathogenicity on cucurbits and eggplants (Huang *et al.*, 2000; Lemaire *et al.*, 1999; LaMondia *et al.*, 1999; Whipps *et al.*, 1998). This founding postulates existence of different pathotypes (*formae speciales*) of this pathogen (Huang *et al.*, 1998b; Huang *et al.*, 2000; Lebeda and Mieslerová, 1999b).
There must be also stressed that host range of *O. lycopersici* is broader and involves representatives of another (and very distant) plant families as Apocynaceae, Asteraceae, Campanulaceae, Crassulaceae, Cistaceae, Dipsacaceae, Linaceae, Malvaceae, Papaveraceae, Pedaliaceae, Scrophulariaceae, Valerianaceae and Violaceae (Lemaire *et al.*, 1999; Whipps *et al.*, 1998).

4. VARIATION IN RESPONSE OF WILD *LYCOPERSICON* SPP. TO *O. LYCOPERSICI*

A set of 154 accessions of nine wild *Lycopersicon* spp. were tested for resistance to Czech isolate of *O. lycopersici*. Screening revealed valuable sources of resistance among *L. hirsutum, L. pennellii, L. chilense, L. peruvianum* and *L. parviflorum*. Mainly some *L. hirsutum* and *L. pennellii* accessions could be considered as "breeding treasure", because stability of their resistance was confirmed by testing with another *O. lycopersici* isolates. On the other hand, all accessions of *L. esculentum* var. *cerasiforme* and *L. pimpinellifolium*, which are closely related to cultivated tomato, showed susceptible reactions to all isolates used. These host genotypes are considered as "universally susceptible", in that they carry no resistances (Mieslerová *et al.*, 2000). The obtained results coincide with recent taxonomic classification and genetic relationships within genus *Lycopersicon* (based on RFLPs) (Miller and Tanksley, 1990).
The data presented here agree with the conlusions of Lindhout *et al.* (1994), who classified *L. hirsutum, L. parviflorum* and *L. pennellii* as resistant (resp. moderately resistant) species. Ciccarese *et al.* (1998), in their large screening, stated that only in *L. peruvianum* accessions did most plants exhibit slight or intermediate disease incidence, while *L. pimpinellifolium* and *L. esculentum* var. *cerasiforme* accessions showed high percentage of seriously diseased plants. Valuable resistance sources were found also by Ignatova *et al.* (1997), Milotay and Dormanns-Simon (1997) and others.

5. INTRASPECIFIC VARIABILITY OF *O. LYCOPERSICI*

From host range studies is evident that intraspecific variation on the level of pathotypes (*formae specialis*) clearly exists (Lebeda and Mieslerová, 2000a). However, our studies also confirmed that *O. lycopersici* isolates may differ in pathogenicity within one plant genus and/or species. Among *L. esculentum* cultivars and lines there was not found significant variation for resistance to *O. lycopersici*, because of their high susceptibility. However, from inoculation experiments on 35 accessions of wild *Lycopersicon* species, comparing *O. lycopersici* isolates from the Czech Republic, Germany, the Netherlands and England, is evident considerable variability within the studied isolates (Lebeda and Mieslerová, 2000b). Surprisingly, the English isolate exhibited strongly differentiated pathogenicity. Possible specificity of interactions host genotype – pathogen isolate is discutable; in most cases the results suggest that resistance in *Lycopersicon* spp. accessions is 'horizontal' (no absolute resistance) rather than 'vertical' (race-specific resistance) controlled by polygenes rather than major genes and similarly differences in pathogenicity of isolates could be explained by their different aggressiveness rather than virulence. More detailed microscopical study and genetic analysis is needed for verifying of hypothesis about genetic basis of these resistances.
This part of our research could be considered as a world priority; only Huang *et al.* (1998b) studied *O. lycopersici* variability, however, only by AFLP analysis. They revealed at least two different patterns related to two types of *O. lycopersici* isolates occurring in the Netherlands. However, this research was not conducted with pathogenicity studies on a set of host genotypes differing in response to *O. lycopersici*.

6. MECHANISMS OF RESISTANCE IN *LYCOPERSICON* SPP. TO *O. LYCOPERSICI*

In our detailed histological studies of infection process of *O. lycopersici*, plant tissue responses and biochemical changes were included ten *Lycopersicon* spp. genotypes.

Although plant genotypes did not efficiently affected conidial germination, early stages of *O. lycopersici* development were strongly influenced by susceptibility or resistance of host tissue. Extent and intensity of necrotic (hypersensitive) response of cells penetrated by haustoria were closely related with level of host plant resistance. Existence of different resistant mechanism not based on hypersensitivity was also confirmed.
Changes in enzymatic activity (peroxidase, catalase, acid phosphatase) during pathogenesis were studied in details. Increasing of peroxidase activity during pathogenesis was detected mainly in moderately resistant accessions and was well correlated with occurrence of necrosis. Increasing of catalase activity (known substrate competitor of peroxidase) was detected in highly resistant accessions, in which the peroxidase changes and occurrence of hypersensitivity were limited (Lebeda *et al.*, 1999; Mieslerová and Lebeda, 1999b). More detailed research of these aspects is recently carried out.
Field resistance was detected in *L. parviflorum* (LA 1322), which showed no symptoms of disease development in glasshouse experiments under natural infection, however in laboratory conditions fast development of the initial stages and sporulation of *O. lycopersici* was recorded (Mieslerová and Lebeda, 2000).
Information regarding known mechanisms of resistance in *Lycopersicon* spp. is also mentioned by Lindhout *et al.* (1994). They described that resistance to *O. lycopersici* in wild *Lycopersicon* species is macroscopically characterized by very low amount of infection, strongly restricted mycelial growth and a lack of sporulation. From histological studies of resistance mechanisms in plants infected by *O. lycopersici* reported by Huang *et al.* (1997, 1998a), is evident that prevailing, however often not completely effective resistance mechanism of *Lycopersicon* spp., is hypersensitive (necrotic) response. Suprisingly, they also confirmed in one accession of *L. parviflorum* existence of field resistance.
Finaly, all mentioned research fields (directions) provide neverending space for next, more structualized and detailed study of this fungus and its host-pathogen interactions. Using combination of classical, biochemical and molecular approaches is needed.

7. REFERENCES

Ciccarese F., Amenduni M., Schiavone D., Cirulli M. 1998. Occurrence and inheritance of resistance to powdery mildew (*Oidium lycopersici*) in *Lycopersicon* species. Plant Pathology 47: 417-419.
Cook R.T.A, Inman A.J., Billings C. 1998. Identification and classification of powdery mildew anamorphs using light and scanning electron microscopy and host range data. Mycological Research 101: 975-1002.
Huang, C.C., Biesheuvel J., Groot T., Niks R., Lindhout P. 1997. Resistance mechanisms to *Oidium lycopersicum*. Abstr. XIII. Meet. EUCARPIA, Tomato Working Group, Jerusalem, Israel, 54.
Huang C.C., Biesheuvel J., Lindhout P., Niks R.E. 2000. Host range of *Oidium lycopersici* occurring in the Netherlands. European Journal of Plant Pathology 106: 465-73.
Huang C.C., Groot T., Meijer-Dekens F., Niks R., Lindhout P. 1998a. Hypersensitivity is the major mechanism of resistance to powdery mildew (*Oidium lycopersicum*) in *Lycopersicon* species. European Journal of Plant Pathology 104: 399-407.
Huang C.C., Lindhout P., Niks R.E. 1998b. Genetic differences in powdery mildews prevailing recently on tomato. 7th International Congress of Plant Pathology, Edinburg, UK, Offered Papers, Abstracts – Vol. 2 (Themes 1 and 2), 2.2.18.
Ignatova S.I., Gorshkova N.S., Tereshonkova T.A. 1997. Powdery mildew of tomato and sources of resistance. Abstr. XII. Meet. EUCARPIA, Tomato Working Group, Jerusalem, Israel, 79.
Jones H.E., Whiips J.M., Thomas B.J., Carver T.L.W., Gurr S.J. 2000. Initial events in the colonisation of tomatoes by *Oidium lycopersici*, a distinct powdery mildew fungus of *Lycopersicon* species. Canadian Journal of Botany 78: 1361-1366.

LaMondia J.A., Smith V.L., Douglas S.M. 1999. Host range of *Oidium lycopersicum* on selected Solanaceous species in Connecticut. Plant Disease 83: 341-344.
Lebeda A, Mieslerová B, 1999a. Identification, occurrence and host range of tomato powdery mildew (*Oidium lycopersici*) in the Czech Republic. Acta Phytopathologica and Entomologica Hungarica 34: 13-25.
Lebeda A., Mieslerová B. 1999b. Morphological characterization and host-range of tomato powdery mildew (*Oidium lycopersici*) originating from the Czech Republic. The First International Powdery Mildew Conference, Avignon, France, Programme and Abstracts,15.
Lebeda A, Mieslerová B, 2000a. Case study of host-pathogen interaction: Tomato (*Lycopersicon* spp.) – tomato powdery mildew (*Oidium lycopersici*). Plant Protection Science 36: 156-62.
Lebeda A., Mieslerová B, 2000b. Sources, mechanisms and effectivity of resistance in wild *Lycopersicon* spp. to tomato powdery mildew (*Oidium lycopersici*). In: Durable Disease Resistance; Key to Sustainable Agriculture. Symposium, Ede-Wageningen, The Netherlands, November 28 – December 1, 2000. Book of Abstracts, p. 40.
Lebeda A., Mieslerová B., Luhová, L. 1999. Resistance mechanisms of wild *Lycopersicon* species against powdery mildew (*Oidium lycopersici*). 2. Symposium Phytomedizin und Pflanzenschutz im Gartenbau, Wien, Austria, 111-113.
Lemaire J.M., Conus M., Burgerjon A., Mas P. 1999. *Oidium lycopersicum*, un nouvel oidium de la tomate. PHM Revue Horticole 4: 21-24.
Lindhout P., Pet G., Beek H. 1994. Screening wild *Lycopersicon* species for resistance to powdery mildew (*Oidium lycopersicum*). Euphytica 72: 43-49.
Mieslerová B., Lebeda A. 1999a. Taxonomy, distribution and biology of the tomato powdery mildew. Journal of Plant Diseases and Protection 106: 140-57.
Mieslerová B., Lebeda A. 1999b. Variability in the early development of tomato powdery mildew (*Oidium lycopersici*) in the host and non-host species. The First International Powdery Mildew Conference, Avignon, France, Programme and Abstracts, 82.
Mieslerová B., Lebeda A. 2000. Comparative study of *Oidium lycopersici* development on wild representatives of *Lycopersicon* spp. Czech Mycology 52: 148-9.
Mieslerová B., Lebeda A., Chetelat R.T. 2000. Variation in response of wild *Lycopersicon* and *Solanum* spp. against tomato powdery mildew (*Oidium lycopersici*). Journal of Phytopathology 148: 303-11.
Miller J.C., Tanksley S.D. 1990. RFLP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon*. Theoretical and Applied Genetics 80: 437-448.
Milotay P., Dormanns-Simon E. 1997. Powdery mildew on tomato in Hungary and some possible sources of resistance. Abstr. XII. Meet. EUCARPIA, Tomato Working Group. Jerusalem, Israel, 60.
Takamatsu S., Hirata T., Sato Y. 1998. Phylogenetic analysis and predicted secondary structures of the rDNA internal transcribed spacers of the powdery mildew fungi (Erysiphaceae). Mycoscience 39: 441-453.
Whipps J.M., Budge S.P., Fenlon J.S. 1998. Characteristics and host range of tomato powdery mildew. Plant Pathology 47: 36-48.