

Powdery mildew of tomato in Qazvin province of Iran: host range, morphological and molecular characterization

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Abstract: Powdery mildew is one of the most important disease concerns of tomato production in different regions of the world, which is caused by different species of Erysiphales. The most important causal agents of which are *Leveillula taurica* and *Oidium neolycopersici*. In the present study tomato farms in Qazvin province were surveyed and tomato leaves with powdery mildew symptoms were collected. After morphological studies in laboratory and using reliable resources, the causal agent of tomato powdery mildew was identified as *Leveillula taurica*. The host range was determined by inoculation of *Leveillula taurica* from tomato on nine species of plants belonging to four different plant families. All cultivars of tomato, eggplant, pepper and cucumber used in this study, showed disease symptoms on their leaf surfaces. Other plant species including potato, alfalfa, sunflower, clover and sainfoin did not get infected by the pathogen. The nucleotide divergence for the rDNA internal transcribed spacers (ITS) region between tomato mildew and 21 other *Leveillula taurica* isolates ranged from 0.00 to 0.031 %. The sequence of ITS region of *Leveillula taurica* from tomato was identical to that of eight isolates from different plant species.

Keywords: *Oidium*, *Leveillula taurica*, Erysiphales, rDNA

Introduction

Tomato powdery mildew is a common disease in the fields and greenhouse-grown tomatoes all over the world. The disease may be caused by at least four different species of Erysiphaceae, including *Golovinomyces orontii* (Castagne) V. P. Heluta, *Leveillula taurica* (Lev.) G. Arnaud, *Oidium lycopersici* Cooke & Massee and *Oidium neolycopersici*

L. Kiss (Burgerjon, *et al.* 1990; Bélanger and Jarvis, 1994; Paulus and Correll, 1991; Correll *et al.*, 1988; Braun, 1987, 1995; Lamondia *et al.*, 1998; Kiss *et al.*, 2001; Jones *et al.*, 2001).

Golovinomyces orontii is common to many host plants in both temperate and tropical regions and is the only ectophytotic fungus on tomato that produces conidia in long chains (Noordeloos and Loerakker, 1989; Kiss *et al.*, 2005). In the late 1970s, a new powdery mildew disease was reported on tomatoes in Japan, Australia, and later from many parts of Europe and North America and has spread rapidly around the world (Price, 1981; Marois

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et al., 2001; Kiss *et al.*, 2005). While others described another oidium anamorph on tomato that produced conidia in chains (Kiss, 1996; Neshev, 1993; Wics and Clare, 1981, Smith, *et al.* 1997; Whipps, *et al.*, 1998). A study of the *Oidium* species world -wide identified two taxa, one of which was found in various locations around the world (except Australia) and was identified as *O. neolycopersici*. This taxon has superficial hyaline hyphae, unbranched conidiophores and doliform conidia that are formed singly or, in high relative humidity, in pseudo-chains of 2-6 conidia (Jones *et al.*, 2000). The other taxon that was found in Australia always formed conidia in chains, retained the name *O. lycopersici* (Jacob *et al.*, 2008; Jones *et al.*, 2001; Kiss *et al.*, 2001).

As we are aware the first record of powdery mildew on tomato plants in Iran is that by Banihashemi and Zakeri (1996) who reported *L. taurica* on tomato for the first time from Shiraz and Karaj. During recent years several specimens of powdery mildews on tomato have been collected and examined by authors from all over the country. Based on specimens from different regions in Iran, we suggest that powdery mildew on tomato is caused by a single species of *Leveillula* and other erysiphaceous fungi have not been documented on this crop in Iran.

L. taurica s. l. is a pathogen of a wide range of host species in warm, arid to semiarid climates. This species has been reported on hosts of different, phylogenetically unrelated plant families including a minimum of 27 economically important crops (Braun, 1987, 1995; Palti 1988). Strains of *L. taurica* from different host families are morphologically rather uniform. However, this species is considered as a complex species (Braun, 1987, 1995; Voytyuk *et al.*, 2009; Khodaparast *et al.*, 2001, 2011). Khodaparast *et al.* (2001, 2011) sequenced ca 600 bp of the ITS regions, including the 5.8S rDNA, of the nu-rDNA gene for 57 specimens of *L. taurica* on different host families. According to their

sequence analysis, *L. taurica* specimens were divided into different clades. These analyses also confirmed that *L. taurica* is unique in the genus, as it exhibits intraspecific gene sequence diversity considerably higher than that in other species. In several cases *L. taurica s. l.* on a certain host plant species has a sequence different from *L. taurica s. l.* on other host plants such as *Acroptilon*, *Artemisia*, *Onobrychis* etc. Moreover different lineages among *L. taurica s. l.* specimens were hardly distinguishable morphologically. In addition more than one genotype occurring on a single host is sometimes possible (Khodaparast *et al.* 2011).

Hence, the real identity of this pathogen needs more investigations on each important host plant. Some attempts for sequencing of rDNA of tomato powdery mildew failed in previous work. The present work combines the use of morphological and molecular tools to identify the *Leveillula* species infecting tomato in Qazvin province.

Material and Methods

Microscopic examination

Field and glasshouse observations of powdery mildew on tomato were made in different regions of Qazvin, during 2009 – 2010 and powdery mildew infected samples were collected.

In the laboratory infected leaves were dried between sheets of paper and were placed in appropriate envelopes. Morphological characteristics of casual agent were observed and microscopic measurements were made directly using an Olympus light microscope equipped with a Sony digital camera. Small pieces of clear adhesive tape were gently applied to infected leaves, and then transferred into lactophenol on a glass slide.

Features such as location of mycelium on the host and morphology of conidia and conidiophores were studied. At least dimensions of 100 conidia and width of conidiophores were measured.

Host range studies

Nineteen varieties of 11 species from four families (Table 2) were used in this study for considering susceptibility to infection by *L. taurica* from tomato as source plant.

Seeds of all the test plants (except potato) were sown in 0.5 – L pots containing pasteurized potting soil mix. Potatoes used for host range studies were grown from seed tubers, and tuber pieces with a single shoot were placed into 12.5 cm pots containing same pasteurized potting soil mix. All plants were fertilized two times a week with N. P. K solution. All plants were inoculated at four – leaf stage for larger leaved plants (cucumber and sunflower) and at eight to 10 leaf stage for small leaved plants (tomato, potato, eggplant, pepper, alfalfa, clover) (Whipps *et al.*, 1998). Field isolates of *L. taurica* were collected from infected commercial tomato plants at Qazvin. Tomato leaves showing infection and sporulation were stored in a plastic bag under cool condition (about 15 °C) and transported to the laboratory (Correll *et al.*, 1987).

Inoculation for all host range experiments was made by shaking four or five heavily mildewed- tomato leaflets over the test plants' leaflets (Huang *et al.*, 2000). The whole plants were enclosed under high humidity plastic tents on a greenhouse bench for 24 hrs (Lamondia *et al.*, 1998; Whipps *et al.*, 1998). Three replicate pots and one control plant was considered for every cultivar

Control plants were placed in the same plastic tents but were not inoculated. After 10 days, all plants were evaluated for symptoms of powdery mildew infection. If no, or very little infection occurred, two leaves of each test plants were marked and re-inoculated.

The temperature during a 24-hrs period was 20 ± 5 °C and the relative humidity was maintained at 85-100 % in the greenhouse.

DNA sequencing

Total DNA was isolated from fresh specimens using pieces of mycelia consisting of conidiophores and conidia by the Chelex

method (Walsh *et al.*, 1991; Hirata and Takamatsu, 1996). A region spanning ITS1, 5.8S, and ITS2 of rDNA was amplified as described by Khodaparast *et al.* (2011). The PCR products were purified using a USB® ExoSAP-IT® PCR Product cleaning kit (USB, USA). The nucleotide sequences of the PCR products were obtained using direct sequencing in an ABI 3730xl sequencer (Applied Biosystems, USA).

Estimates of evolutionary divergence between sequences

Pair-wise percentages of sequence divergence of the ITS1-5.8S-ITS2 region between sequences were calculated using the Kimura 2-parameter model in MEGA5 (Tamura *et al.*, 2007). All positions containing gaps and missing data were eliminated. There were a total of 496 positions in the final dataset.

Phylogenetic analysis

The obtained sequences were initially inspected manually and visually and aligned using the Genedoc software (Nicholas and Nicholas, 1997). The data were analyzed using the minimum evolution using MEGA version 5 (Tamura *et al.*, 2007). In minimum-evolution method, the evolutionary distances were computed using the Maximum Composite Likelihood method. All positions containing gaps and missing data were eliminated from the dataset (Complete deletion option). All nucleotide substitutions were equally weighted and unordered. The strength of the internal branches from the resulting trees was statistically tested by bootstrap analysis with 1000 replicates (Felsenstein, 1985). Sequences of two *Phyllactinia* species were used as outgroup taxa.

Results and discussion

Morphological examination

In the present study, the causal agent of tomato powdery mildew was characterized by having lanceolate, ellipsoid-lanceolate to

subcylindric primary conidia and cylindrical to subcylindrical secondary conidia (Fig. 1). This mildew has earlier been reported from several specimens on different plant species (Khodaparast *et al.*, 2001, 2011). Dimensions of conidia measurements were 40.8-75.2 x 10.4-23.2 μm and 37.6-74.4 x 11.2-45.6 μm for the primary and secondary conidia, respectively. Width of conidiophores ranged from 4 to 8.8 μm in the widest part of measured samples. The teleomorph of this pathogen was not found in Qazvin.

Estimates of Evolutionary Divergence between Sequences

The numbers of base substitutions per site from tomato and 21 closely related isolates are shown in Table 1. The nucleotide divergence for the ITS region between tomato and other 21 isolates ranged from 0.00 to 0.031 %. Of the 21 isolates of *L. taurica s. lat.*, the divergence between tomato isolate and 8 isolates from different plant families such as Elaeagnaceae, Fabaceae, Amarantaceae, Euphorbiaceae etc. was 0.00 % (Table 1).



Figure 1 Conidia of *Leveillula taurica* from *Lycopersicon esculentum*, scale bar = 50 μm .

Table 1 Estimates of Evolutionary Divergence between Sequences of tomato and 21 closely related isolates of *Leveillula taurica*. Analyses were conducted using the Kimura 2-parameter method in MEGA5. All positions containing alignment gaps and missing data were eliminated only in pairwise sequence comparisons (pair-wise deletion option). There were a total of 496 positions in the final dataset.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| [1] | | | | | | | | | | | | | | | | | | | | | |
| [2] | 0.002 | | | | | | | | | | | | | | | | | | | | |
| [3] | 0.031 | 0.033 | | | | | | | | | | | | | | | | | | | |
| [4] | 0.000 | 0.002 | 0.031 | | | | | | | | | | | | | | | | | | |
| [5] | 0.000 | 0.002 | 0.031 | 0.000 | | | | | | | | | | | | | | | | | |
| [6] | 0.000 | 0.002 | 0.031 | 0.000 | 0.000 | | | | | | | | | | | | | | | | |
| [7] | 0.000 | 0.002 | 0.031 | 0.000 | 0.000 | 0.000 | | | | | | | | | | | | | | | |
| [8] | 0.000 | 0.002 | 0.031 | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | | | | | | | | | |
| [9] | 0.000 | 0.002 | 0.031 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | | | | | | | | |
| [10] | 0.000 | 0.002 | 0.031 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | | | | | | | | | | | | |
| [11] | 0.002 | 0.004 | 0.033 | 0.002 | 0.002 | 0.002 | 0.002 | 0.002 | 0.002 | 0.002 | | | | | | | | | | | |
| [12] | 0.004 | 0.005 | 0.035 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.005 | | | | | | | | | | |
| [13] | 0.002 | 0.004 | 0.033 | 0.002 | 0.002 | 0.002 | 0.002 | 0.002 | 0.002 | 0.002 | 0.004 | 0.005 | | | | | | | | | |
| [14] | 0.004 | 0.005 | 0.035 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.004 | 0.005 | 0.007 | 0.005 | | | | | | | | |
| [15] | 0.005 | 0.007 | 0.037 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.005 | 0.007 | 0.009 | 0.007 | 0.009 | | | | | | | |
| [16] | 0.007 | 0.005 | 0.039 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.009 | 0.011 | 0.009 | 0.011 | 0.013 | | | | | | |
| [17] | 0.007 | 0.009 | 0.039 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.007 | 0.009 | 0.011 | 0.009 | 0.011 | 0.013 | 0.011 | | | | | |
| [18] | 0.009 | 0.011 | 0.041 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.011 | 0.013 | 0.011 | 0.013 | 0.014 | 0.013 | 0.002 | | | | |
| [19] | 0.011 | 0.013 | 0.041 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.013 | 0.014 | 0.013 | 0.013 | 0.016 | 0.016 | 0.007 | 0.009 | | | |
| [20] | 0.011 | 0.013 | 0.041 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.011 | 0.013 | 0.014 | 0.013 | 0.013 | 0.016 | 0.016 | 0.007 | 0.009 | 0.000 | | |
| [21] | 0.009 | 0.011 | 0.041 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.009 | 0.011 | 0.013 | 0.011 | 0.011 | 0.014 | 0.014 | 0.005 | 0.007 | 0.002 | 0.002 | |
| [22] | 0.000 | 0.002 | 0.031 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.002 | 0.004 | 0.002 | 0.004 | 0.005 | 0.007 | 0.007 | 0.009 | 0.011 | 0.011 | 0.009 |

[1] *L. taurica ex Elaeagnus*, [2] *Daphne*, [3] *Helianthus_Salmas*, [4] *Glycyrrhiza*, [5] *Celosia*, [6] *Peganum*, [7] *Chrozophora*, [8] *Haplophylum*, [9] *Zygophyllum*, [10] *Caparis*, [11] *Alhagi*, [12] *Lotus*, [13] *Euphorbia*, [14] *Ononis*, [15] *Allium*, [16] *Eryngium*, [17] *Carthamus*, [18] *Epilobium*, [19] *Vicia*, [20] *Polianthes* [21] *Medicago*, [22] *Lycopersicon*

Phylogenetic analysis

One newly determined sequence was aligned with 44 further sequences of *Leveillula* already reported by Khodaparast *et al.* (2001, 2007, 2011) and retrieved from DNA database (NCBI). There were a total of 496 positions in the final dataset.

According to Khodaparast *et al.* (2011) *Leveillula* specimens were divided into several clades. Moreover, about 35 *Leveillula* isolates

from plant species belonging to different plant families clustered together in a weakly supported clade (clade 1 in Khodaparast *et al.*, 2011 and Fig. 2). Based on this study *Leveillula* specimen on tomato analyzed in this study also clustered into clade 1 reported by Khodaparast *et al.* (2011).

Most of taxa in this clade were characterized with lanceolate to ellipsoid-lanceolate primary conidia as shown for tomato powdery mildew in this study.



Figure 2 A minimum-evolution (ME) tree (length = 0.36098138) based on ITS data for 45 *Leveillula* taxa and two outgroup taxa. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were computed using the Maximum Composite Likelihood method and are in the units of the number of base substitutions per site. The ME tree was searched using the Close-Neighbor-Interchange (CNI) algorithm at a search level of 1 (level = 1). The Neighbor-joining algorithm was used to generate the initial tree. All positions containing gaps and missing data were eliminated from the dataset (Complete deletion option). The numbers above the branches represent branch support using 1000 bootstrap replications (Bootstrap values below 50 % are not shown).

Host range studies

All tomato varieties, eggplant, pepper and cucumber tested in this study showed disease symptoms on their leaf surface. The first symptoms appeared on leaves as bright yellow spots. The spots enlarged and eventually turned to brown. Lesions were not observed on any of the uninoculated control plants. The other plant species were not infected by powdery mildew pathogen in these experiments (Table 2).

Table 2 Host range test of tomato powdery mildew (*Leveillula taurica*).

| Family | Species | Common name | Variety | Reaction | | |
|---------------------------|---|----------------|--------------------------|----------|---------|---|
| Solanaceae | <i>Lycopersicon esculentum</i> ¹ | Tomato | Super crystal B | + | | |
| | | | Super Strain B | + | | |
| | | | Early Urbana | + | | |
| | | | Calj | + | | |
| | | | Superchef | + | | |
| | | | Kimia | + | | |
| | | | Falcato | + | | |
| | | | <i>Solanum tuberosum</i> | potato | Savalan | - |
| | | | <i>Solanum melongena</i> | eggplant | Varamin | + |
| | | | | | Yazd | + |
| Solanaceae | <i>Capsicum frutescens</i> | cayenne pepper | Semnan | + | | |
| | | | bell pepper | Colombo | + | |
| | | | | | | |
| Fabaceae | <i>Medicago sativa</i> | alfalfa | Hamedani | - | | |
| | | | Native | - | | |
| | <i>Trifolium resupinatum</i> | clover | Variety | - | | |
| | | | | | | |
| | <i>Trifolium pratense</i> | red clover | Redqueen | - | | |
| <i>Onobrychis aucheri</i> | sainfoin | unknown | - | | | |
| Asteraceae | <i>Helianthus annuus</i> | sunflower | Azargol | - | | |
| | | | Progress | - | | |
| Cucurbitaceae | <i>Cucumis sativus</i> | cucumber | unknown | + | | |

+ = positive infection, - = no infection

1. Field isolates of tomato powdery mildew used as inoculum source.

The size and shape of conidia of the *L. taurica* isolates formed on test plants were identical to those that formed on tomato in the field. The data showed that *L. taurica* is capable of infecting a group of plant species under favorable environmental conditions. The families including Fabaceae and Asteraceae didn't show any lesions after two

times of inoculation. Different inoculated plants did not develop powdery mildew on their leaves at the same time and same severity. For instance, all cultivars of inoculated tomatoes were severely affected by powdery mildew about 12 days after colonies first appeared, while a few diffuse colonies formed on the pepper leaves about 20-26 days after first symptoms were observed.

Thomson and Jones (1981) have reported the fungus also infects alfalfa and potato. But in this study we couldn't observe any symptoms of infection on potato or alfalfa. Palti (1988) mentioned that there is much difference in the degree of sensitivity among various hosts and that different isolates of this fungus in distinct hosts are able to infect plants of the same family and also those of other families.

The differences in the reaction of test plants may be due to differences in host genotypes, the race of the pathogen being examined and the environmental conditions. Due to experimental limitations we were not able to determine which factor affects the experiments? However, three plant species belonging to genera other than *Lycopersicon* were susceptible to *L. taurica* suggesting that this pathogen may infect plants other than tomato, even plants out of Solanaceae such as Cucurbitaceae.

Tomato is a major host of *L. taurica* in warm arid to semiarid climates (Correll *et al.*, 1987; Palti, 1971). Our findings showed that *L. taurica* is widespread in Qazvin. We found that disease was destructive in all of the tomato growing regions during 2009 - 2010. Although this disease has previously been reported on tomatoes, this is the first extended report of this pathogen as the important causal agent of powdery mildew on tomatoes in Iran.

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سفیدک پودری گوجه‌فرنگی در استان قزوین: دامنه میزبانی، مشخصات ریخت‌شناسی و مولکولی

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چکیده: سفیدک پودری یکی از مهم‌ترین بیماری‌های گوجه‌فرنگی در مناطق تولید این محصول است که توسط گونه‌های مختلف راسته Erysiphales ایجاد می‌شود که مهم‌ترین گونه‌های آن *Leveillula taurica* و *Oidium neolycopersici* هستند. در این مطالعه مزارع گوجه‌فرنگی در استان قزوین مورد بررسی قرار گرفتند و برگ‌های آلوده این گیاه به سفیدک سطحی جمع‌آوری شدند. بعد از مطالعات ریخت‌شناسی و با استفاده از منابع معتبر فقط *Leveillula taurica* به‌عنوان عامل سفیدک سطحی گوجه‌فرنگی در قزوین شناسایی شد. همچنین دامنه میزبانی جدایه گوجه‌فرنگی روی نه گونه گیاهی متعلق به چهار تیره گیاهی بررسی شد. همه ارقام گوجه‌فرنگی، بادنجان، فلفل و خیار در این مطالعه علائم آلودگی را روی برگ‌های خود نشان دادند. گونه‌های دیگر شامل سیب‌زمینی، یونجه، آفتابگردان، شبدر و اسپرس توسط قارچ آلوده نشدند. تفاوت در توالی ناحیه ITS روی دی ان ای ریبوزومی بین جدایه گوجه‌فرنگی و ۲۱ جدایه دیگر *Leveillula taurica* صفر تا ۰/۰۳۱ درصد بود. توالی این نمونه با توالی هشت نمونه جدا شده از میزبان‌های دیگر کاملاً یکسان بود.

واژگان کلیدی: *Oidium*, *Leveillula taurica*, Erysiphales, rDNA