



Fusarium oxysporum f. sp. *lavandulae*, a novel *forma specialis* causing wilt on *Lavandula* × *allardii*

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Published online: 2 July 2018
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Abstract

Symptoms of a vascular wilt were observed on many plants of *Lavandula* × *allardii* (hybrid of *Lavandula dentata* and *L. latifolia*) cultivated in a nursery near Albenga, Liguria region, Northern Italy. After identification based on morphological characteristic and ITS sequence analysis, the pathogen was identified as *Fusarium oxysporum*. Eight single-spore isolates obtained from infected tissues were used for a phylogenetic analysis in order to identify the *forma specialis*. Translation elongation factor 1- α (*EF-1 α*), intergenic spacer (IGS) and three genes encoding for polygalacturonase genes (*pg1*, *pg5* and *pgx1*) were amplified by PCR. Gene sequences were aligned with other *formae speciales* of *Fusarium oxysporum* obtained from GenBank databases in order to build phylogenetic trees. Results obtained for each genomic region showed a unique group with isolates derived from *L. × allardii* well separated from the other *formae speciales*. Results obtained, together with pathogenicity tests, allowed us to introduce a new *forma specialis* named *F. oxysporum* f. sp. *lavandulae*.

Keywords Ornamental plants · Fusarium wilt · Elongation factor 1- α · Intergenic spacer · Endopolygalacturonase

Introduction

The genus *Lavandula* (Lamiaceae) includes at least 34 different species, self-sown in the Mediterranean basin (Miller 1985). Among these, the most used in traditional medicine (Gámez et al. 1987) and/or in pharmaceutical and cosmetic industries (Cavanagh and Wilkinson 2002) are: *Lavandula angustifolia* Mill. (Lavender), *L. latifolia* Medik., *L. fragrans* L. (*L. angustifolia* × *L. latifolia*), *L. stoechas* L. and *L. multifida* L. *Lavandula* × *allardii* is a hybrid of *L. dentata* and *L. latifolia*, commonly used as ornamental plant. This species presents long light purple flowers separated with small bracts on stems 35–45 cm long. The toothed leaf color could be considered a soft grey green and the blooms appear in early summer.

The main diseases of the *Lavandula* genus are caused by different *Phytophthora* (*P. nicotianae*, *P. pelgrandis*, *P. palmivora* and *P. parassitica*) and *Pythium* species (Faedda et al. 2013; Davino et al. 2002; Putnam 1991). Additionally, infections by *Fusarium sporotrichioides* and *Fusarium solani* were found in different species of *Lavandula* (Cosic et al. 2012; Ren et al. 2008), while *Fusarium oxysporum* was described on *L. pubescens* (Perveen and Bokhari 2010).

During December 2014, 14-month-old plants of tree-shaped *L. × allardii* grown in pots in a nursery located in Regione Carenda near Albenga (Northern Italy) at 0 m below sea level (GPS coordinates: 44.074558 North, 8.219336 East) showed symptoms of a previously unknown wilt. The disease affected 70% of 4000 plants. Symptoms consisted of chlorosis and yellowing of leaves, followed by wilting of leaves and branches (Fig. 1a). Brown discoloration was observed in the vascular stem system (Fig. 1b). The fungal causal agent of the disease was isolated from symptomatic vascular tissues. The pathogen was identified as *F. oxysporum* by morphological and molecular assays and the Koch's postulates were fulfilled (Garibaldi et al. 2015).

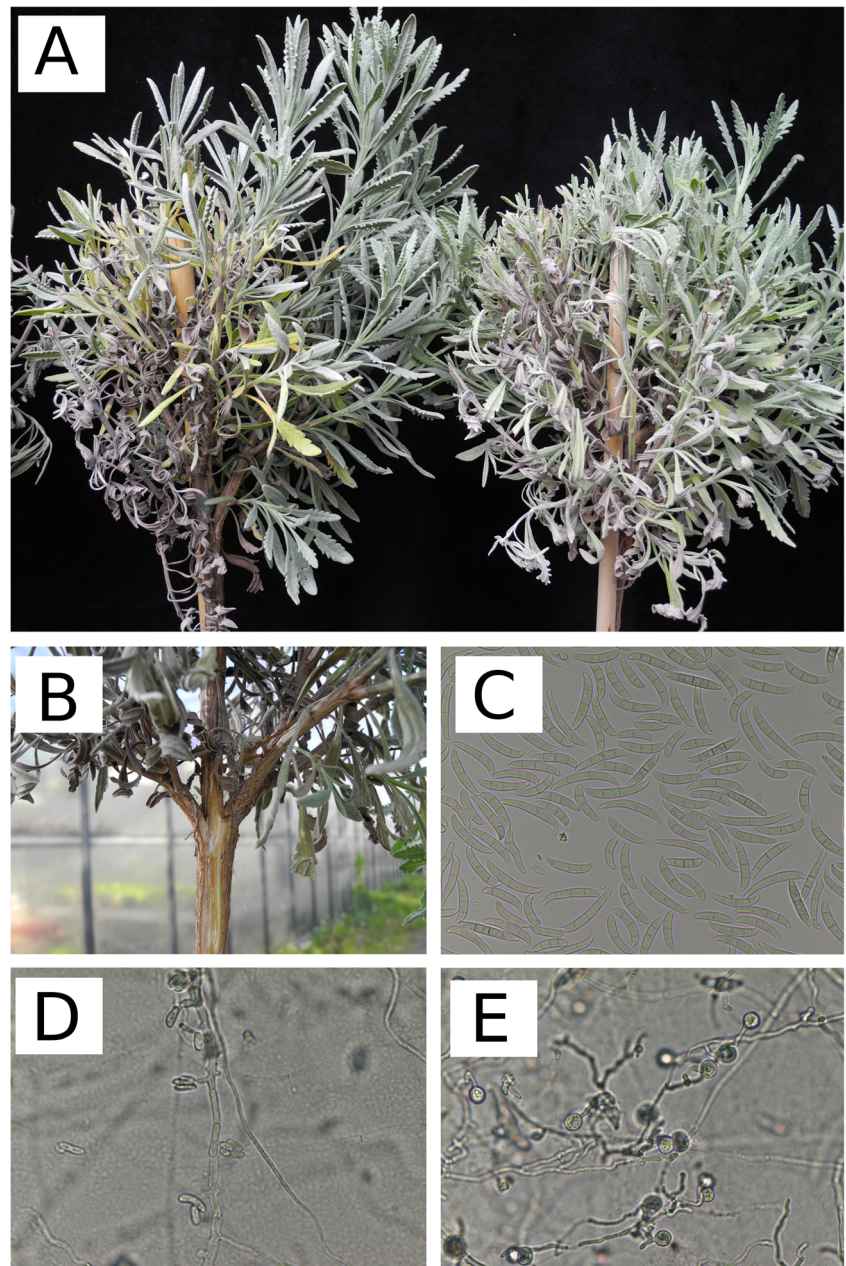
F. oxysporum is one of the most important plant pathogens, causing wilt on economically important

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Fig. 1 Chlorosis, yellowing and wilts caused by *Fusarium oxysporum* on naturally affected plants of *Lavandula × allardii* (a). Stem tissues of *Lavandula × allardii* with vascular browning caused by *Fusarium oxysporum* (b). Three-septate, slightly falcate macroconidia (c). Short monophialides with unicellular, ovoid-elliptical microconidia (d) and chlamydospores (e) of *Fusarium oxysporum* isolated from *Lavandula × allardii*



vegetable and ornamental crops (Gullino et al. 2012). About 130 different *formae speciales* of this pathogen have been described (Armstrong and Armstrong 1981; O'Donnell and Cigelnik 1999; Baayen et al. 2000; O'Donnell et al. 2009; Leslie 2012). The identification of *formae speciales* is commonly based on pathogenicity assays (Recorbet et al. 2003) and supported by molecular identification tools (Lievens et al. 2012).

In this work, a phylogenetic study was performed in order to identify the *forma specialis* of *F. oxysporum* able to infect *L. × allardii*.

Materials and methods

Single-spore isolates *F. oxysporum* isolates were obtained from affected plants of *L. × allardii* collected in the nursery reported above, by plating little pieces of affected vascular tissues onto potato dextrose agar (PDA) medium amended with streptomycin sulphate (0.025 mg ml^{-1}). The isolates produced a white to pale violet mycelium with pale purple pigments in the agar medium and short monophialides with unicellular, ovoid-elliptical microconidia. Successively, each isolate was grown on potato dextrose broth (PDB) (Liofilchem)

Table 1 *Fusarium oxysporum* single-isolates from *Lavandula × allardii* used in this study

| Isolates | Year | Place |
|----------|------|---------------------------|
| Folav 1 | 2014 | Albenga* - Northern Italy |
| Folav 2 | 2014 | Albenga* - Northern Italy |
| Folav 3 | 2014 | Albenga* - Northern Italy |
| Folav 4 | 2014 | Albenga* - Northern Italy |
| Folav 5 | 2014 | Albenga* - Northern Italy |
| Folav 6 | 2014 | Albenga* - Northern Italy |
| Folav 7 | 2014 | Albenga* - Northern Italy |
| Folav 8 | 2014 | Albenga* - Northern Italy |

*Regione Carenza (GPS coordinates: 44.074558 North, 8.219336 East)

to distribute the serial dilution of conidial suspensions onto PDA medium. Using a stereomicroscope, single germinated microconidia were selected and transferred onto PDA plates to obtain single-spore cultures. The single-spore isolates of *F. oxysporum* from *L. × allardii* used in this work are listed in Table 1. On PDA, single-isolates of *F. oxysporum* from *L. × allardii* produced microconidia measuring 4.8–13.1 × 2.3–4.5 (mean 7.4 × 3.3) μm (Fig. 1d). On carnation leaf agar (CLA) (Fisher et al. 1982), slightly falcate macroconidia were produced in pale orange sporodochia. Macroconidia had 3-septa, a foot-shaped basal cell, a short apical cell, and measured 19.6–39.2 × 2.7–4.6 (mean 27.0 × 3.6) μm (Fig. 1c). On the same medium, terminal and intercalary chlamydospores were observed that appeared rough walled, mostly singles, 6.2–9.8 (mean 7.9) μm in diam (Fig. 1e). (Garibaldi et al. 2015).

Pathogenicity assays Pathogenicity assays were performed with all the isolates listed in Table 1. The inoculum of each isolate was obtained in PDB, shaking cultures (90 rpm) for 10 days at 25 °C ± 1, with 12 h of fluorescent light and 12 h of dark per day. Successively, all the suspensions were filtered and the conidial concentrations were determined with a haemocytometer. Then, conidial suspensions were adjusted with deionized water to obtain the final concentration of 1 ×

10⁷ conidia/ml used in the assays. Six 11-month-old healthy plants of *L. × allardii* were inoculated for each isolate by dipping roots in the suspension without injuring their tissues. Six plants were dipped only in sterilized water and used as controls. Successively, plants were transplanted in 2-l pots containing a substrate (sphagnum peat:perlite:pine and bark:clay; 50:20:20:10) previously steam-sterilized and transferred to a greenhouse, at temperatures ranging from 25 to 31 °C.

DNA extraction Genomic DNA extraction was carried out by using a commercial kit (Omega Bio-Tek), according to the manufacturer's instructions. For each isolate, fresh mycelium was obtained by 50 ml culture on PDB incubated at 25 °C. After 6 days, the cultures were filtered and approximately 50 mg of mycelium was transferred into a 2 ml tube containing 400 μl of lysis buffer and two tungsten beads (Stainless Steel Beads, 5 mm, Qiagen, Hilden, Germany). Mycelium was homogenized using Qiagen Tissue Lyser for 3 min, at 28 repetitions per minute and the lysate obtained was used for DNA extraction. DNA concentration was measured using a (Thermo USA) spectrophotometer, and the extracted DNA was stored at –20 °C until further use.

PCR amplification Five different regions were used for the phylogenetic analysis. In particular the elongation factor 1 α (*EF-1α*), three polygalacturonase genes (*pg1*, *pg5* and *pgx1*) and finally the intergenic spacer (IGS), were amplified. PCR reactions were performed with the primers reported on Table 2. The same amplification conditions were used for *EF-1α*, *pg1*, *pg5* and *pgx1* using a Thermal cycler (Biorad) in a 20 μl reaction mixture containing: 10 ng of gDNA, 0.5 μM of each primer, 1 U of *Taq* DNA polymerase (Qiagen), 2 μL of PCR buffer 10×, 1 μl of dNTPs stock (final concentration 0.25 mM), and 0.8 μl of MgCl₂ (final concentration 1 mM). The cycling conditions included an initial denaturing step at 94 °C for 5 min, followed by 50 cycles of denaturation at 94 °C for 1 min, annealing at 52 °C for 1 min, extension at 72 °C for 2 min, and final extension at 72 °C for

Table 2 List of primers used in this study

| Gene | Primer | Nucleotide Sequences (5' → 3') | Source |
|--------------|--------|--------------------------------|-----------------------|
| <i>EF-1α</i> | Ef1 | ATGGGTAAGGAAGACAAGAC | O'Donnell et al. 1998 |
| | Ef2 | GGAAGTACCAAGTGATCATGTT | |
| IGS | CNL12 | CTGAACGCCTCTAAGTCAG | Appel and Gordon 1995 |
| | CNS1 | GAGACAAGCATATGACTACTG | |
| <i>pg1</i> | endoF | CCAGAGTGCCGATACCGATT | Hirano and Arie 2009 |
| | endoR2 | GCTTAGYGAACAKGGAGTG | |
| <i>pg5</i> | PG2F | AGATGCAAGGCCGATGATGT | Hirano and Arie 2009 |
| | PG2R | TCCATGTACTTCTCCTCACC | |
| <i>pgx1</i> | PgxF | TCGTGGGGTAAAGCGTGGT | Hirano and Arie 2009 |
| | PgxR | TTACTATAGGTCGATCAGCC | |

Table 3 Accession numbers of sequences deposited in GenBank

| Isolates | Accession Numbers in GenBank | | | | |
|----------|--------------------------------|------------|------------|------------|-------------|
| | <i>EF-1α</i> | <i>IGS</i> | <i>pgl</i> | <i>pg5</i> | <i>pgx1</i> |
| Folav 1 | KT897684 | KT897652 | KT897660 | KT897668 | KT897676 |
| Folav 2 | KT897685 | KT897653 | KT897661 | KT897669 | KT897677 |
| Folav 3 | KT897686 | KT897654 | KT897662 | KT897670 | KT897678 |
| Folav 4 | KT897687 | KT897655 | KT897663 | KT897671 | KT897679 |
| Folav 5 | KT897688 | KT897656 | KT897664 | KT897672 | KT897680 |
| Folav 6 | KT897689 | KT897657 | KT897665 | KT897673 | KT897681 |
| Folav 7 | KT897690 | KT897658 | KT897666 | KT897674 | KT897682 |
| Folav 8 | KT897691 | KT897659 | KT897667 | KT897675 | KT897683 |

7 min. For IGS amplification a PCR reaction was performed in a 50 μ l reaction mixture containing: 30 ng of gDNA, 5 μ l of

10 μ M stock (final concentration 1 μ M) of each primer, 3 unit of *Taq* DNA polymerase (Qiagen), 5 μ l of PCR buffer 10 \times , 5 μ l of dNTPs stock (final concentration 0.25 mM), and 10 μ l of 5X Q solution (for amplified a G-C rich regions). A negative control (no template DNA) was included in all experiments. PCR profile were analyzed via 1% agarose gel (Agarose D-1 LOW EEO, Eppendorf). After purification with QIAquick PCR purification kit (Qiagen, Hilden, Germany), purified PCR bands were sequenced via BigDye Direct Sanger Sequencing Kit (Thermo Fisher, Waltham, Massachusetts, USA). *EF-1 α* , *pgl*, *pg5* and *pgx1* regions were sequenced in both directions while for the IGS region we used also two internal primers: CNS12 (GCACGCCAGGACTGCCTCGT) and RU46.67 (GTGTGGCGTGCTTGTATT) (Mbofung et al. 2007). Sequences were deposited at GenBank and accession numbers are given in Table 3.

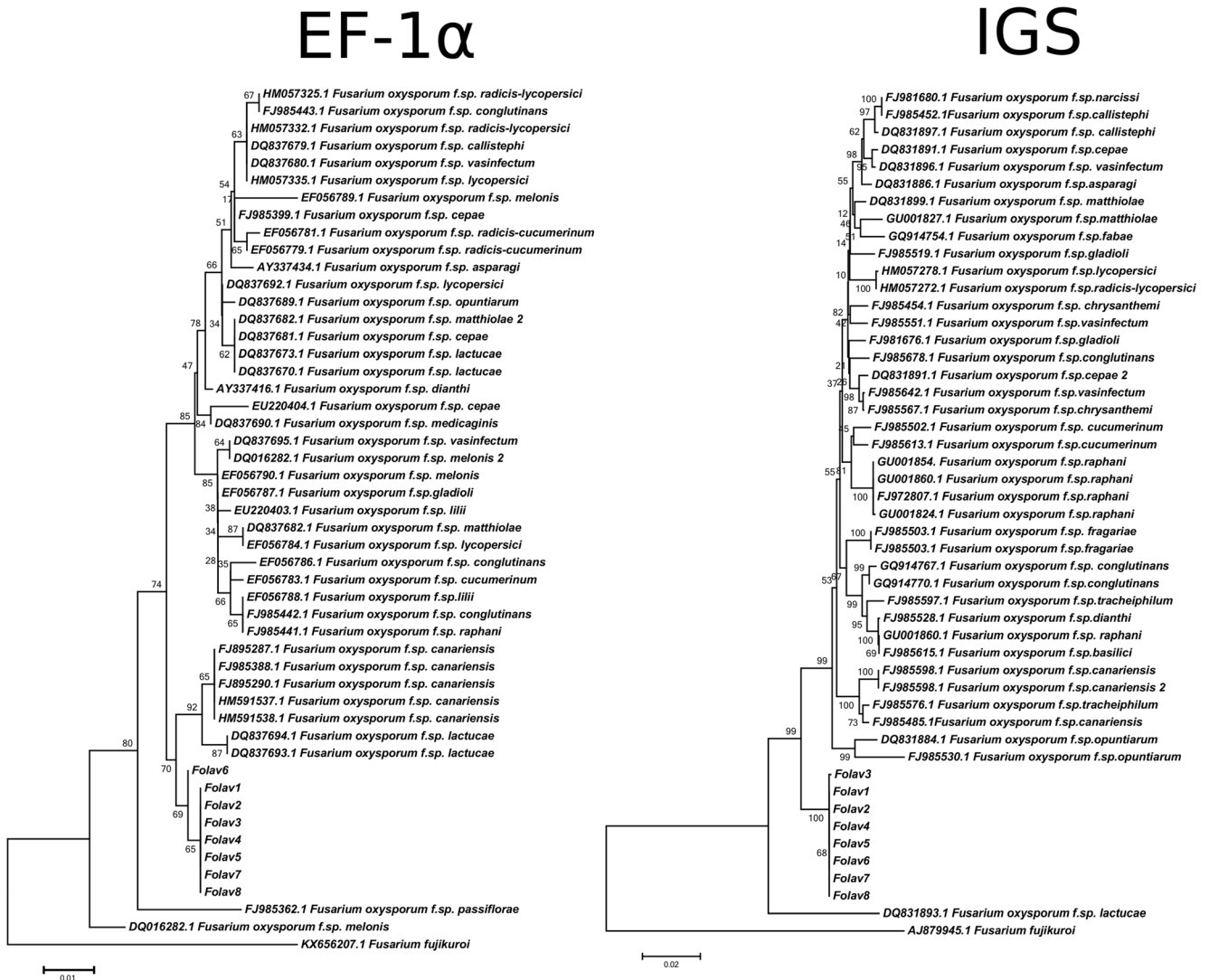


Fig. 2 Phylogenetic tree based on *EF-1 α* and IGS sequences, built by Mega6 software with the Neighbor joining method with 1000 bootstrapping replicates. All samples were included in the analysis

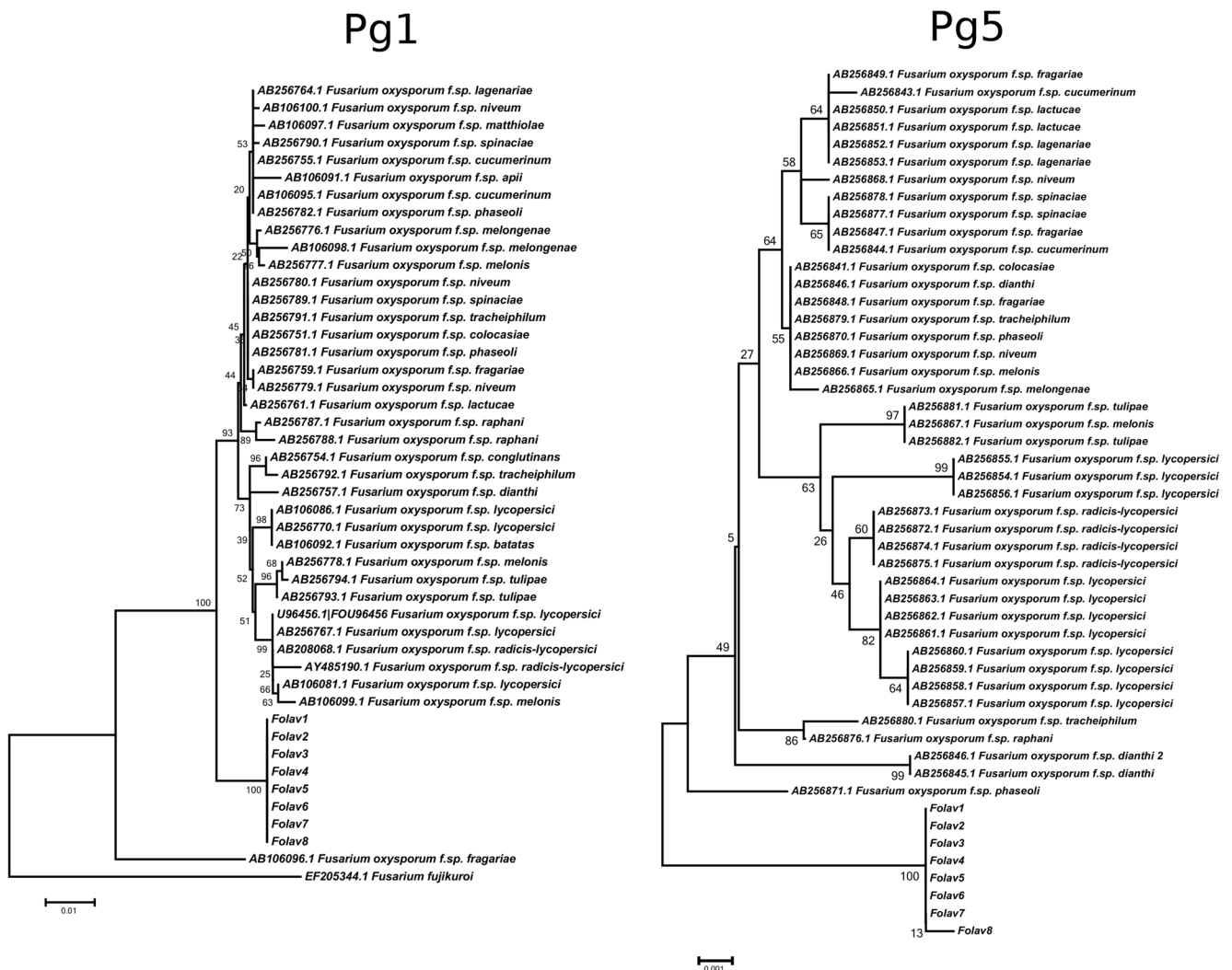


Fig. 3 Phylogenetic tree based on *pg1* and *pg5* gene sequences, built by Mega6 software with the Neighbor joining method with 1000 bootstrapping replicates. All samples were included in the analysis

Alignment and phylogenetic analyses Similarity searches (BLASTN, default parameters) were performed for all sequences. The sequences obtained were used for CLUSTALW multiple sequence alignments through MEGA6 software set to default parameters. Manual corrections were performed for each alignment in order to delete trimmer regions outside and discard incomplete sequences. Phylogenetic trees for each genomic region were constructed in MEGA6 (Tamura et al. 2013) using the Neighbor joining method with 1000 bootstrap repeats with pairwise deletion option. The evolutionary distances were computed using the Tajima-Nei method and are in the units of the number of base substitutions per site. In each analysis all samples were included together with sequences derived from different *F. oxysporum formae speciales* obtained from the GenBank database.

Results

Pathogenicity assay About 40 days after the inoculation, first symptoms of wilting appeared on leaves of plants of *L. × allardii* inoculated with the isolates Folav-1, Folav-2, Folav-3, Folav-4. Successively, symptoms appeared also on plants inoculated with the isolates Folav-5, Folav-6, Folav-7 and Folav-8. When the disease progressed, twigs and stems wilted, vascular tissues were discoloured and plants died about 60 days after the artificial inoculation. *F. oxysporum* was reisolated from plants inoculated with all the isolates, while controls remained symptomless.

Molecular phylogenetic analysis of EF-1α region Amplification of the *EF-1α*, gene resulted in 750 bp fragments of DNA. After multialignment with other *formae speciales* present on GenBank, a portion of 413 bp was used

for the phylogenetic analyses. The results obtained showed that isolates obtained from *L. × allardii* were well distinct from other *formae speciales* supported by a 67 bootstrap value (Fig. 2). Sequence used showed an 0.022 distance mean with 0.002 of standard error. Sequences used for the phylogenetic analysis were deposited on GenBank (Table 3).

Molecular phylogenetic analysis of IGS region As observed on *EF 1- α* analysis, also in this case all isolates from *L. × allardii* grouped together separated from other *formae speciales* present on GenBank with a strong bootstrap value (100) (Fig. 2). Sequence used showed an 0.032 distance mean with 0.002 of standard error. A 1994 bp sequence were obtained for each isolate and the sequences used for the phylogenetic analysis were deposited in GenBank (Table 3).

Molecular phylogenetic analysis of endo- and exopolygalacturonase In order to confirm the previous results, three different genes encoding for two endopolygalacturonase (*pg1* and *pg5*) and one exopolygalacturonase (*pgx1*) we used. Once again, the results confirmed what had been observed in the previous phylogenetic analysis (Fig. 3; Fig. 4). We used a portion of these gene and in particular 903 bp for *pg1* gene, 1225 bp for *pg5* and finally 1602 bp for *pgx1*. All results obtained from these sequences showed again a well separated group for the *L. × allardii* isolates with strong bootstrap value (99 for *pgx1*, 100 for *pg1* and *pg5*). Phylogenetic tree was obtained with distance mean of 0.028 for *pgx1* 0.018 for *pg1* and 0.07 for *pg5* and respectively standard error of 0.002 for *pgx1* and *pg1* and 0.001 for *pg5*.

Discussion

In this work, a new *F. oxysporum* was isolated from *L. × allardii* plants showing severe wilt symptoms in a nursery located in North Italy. Virulence of all isolates was verified by pathogenicity assay performed in greenhouse and Koch's postulates were fulfilled. Specialization on different host plants is a well-known characteristic of *F. oxysporum* (Gordon and Martyn 1997). However, the high presence of different transposable elements (Daboussi and Capy 2003) allows *F. oxysporum* to rearrange his genome, in relation with the selection pressure and the intensive cultivations of host plants. The horizontal transfer of pathogenicity genes is well-known for *F. oxysporum* species complex (Van der Does and Rep 2007). Therefore, the intensive cultivation of a large number of ornamentals offers to *F. oxysporum* the possibility of new specializations. In the last years, three new *formae speciales* have been identified in Italy by phylogenetic analysis based on endopolygalacturonase and exopolygalacturonase genes: *F. oxysporum* f. sp. *crassulae* on *Crassula ovata* (Ortu et al. 2013), *F. oxysporum* f. sp.

pgx4

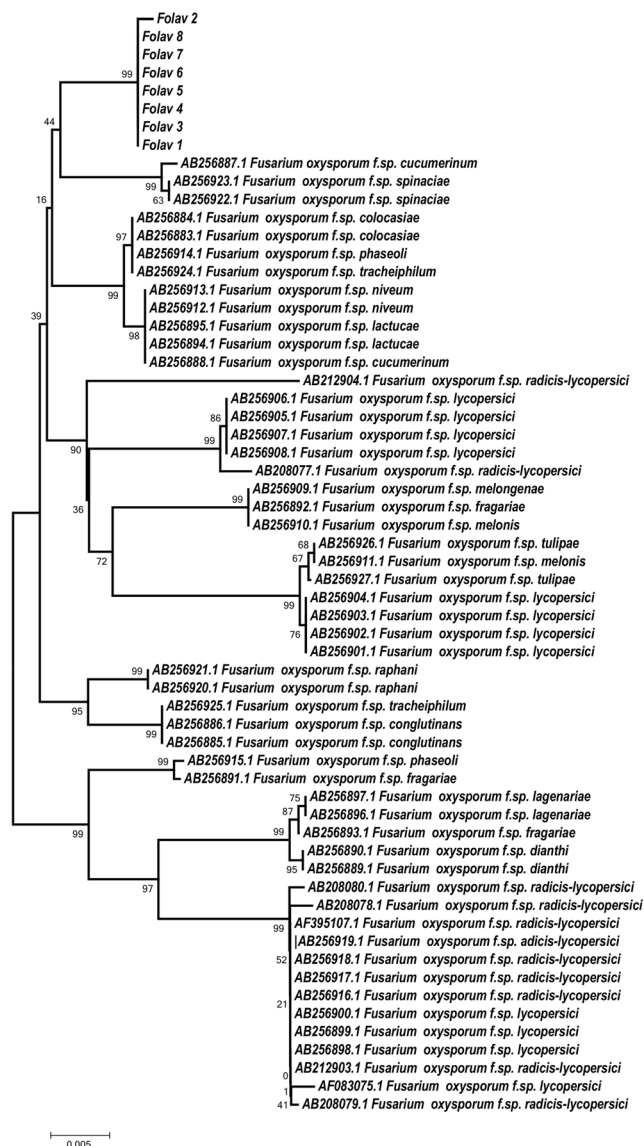


Fig. 4 Phylogenetic tree based on *pgx1* gene sequences, built by Mega6 software with the Neighbor joining method with 1000 bootstrapping replicates. All samples were included in the analysis

echeveriae on *Echeveria agavoides* (Ortu et al. 2015a) and *F. oxysporum* f. sp. *papaveris* on *Papaver nudicaule* (Ortu et al. 2015b). In this work, phylogenetic analyses based on five different genomic regions have identified a new *forma specialis* of *F. oxysporum* on *L. × allardii* never described before. We propose this to be named *F. oxysporum* Schlechtendal f. sp. *lavandulae* f. sp. nov.

More studies should be done about the epidemiology of *F. oxysporum* on *L. × allardii*, in particular about the effect of temperature on the disease development. Also, the susceptibility of species and cultivars of *Lavandula* to this new *forma specialis* of *F. oxysporum* should be investigated to provide

useful information to the growers of these crop. In fact, the growing of *L. × allardii* is still limited, contrary to *L. officinalis* and *L. stoechas* that are largely cultivated in Liguria region where the disease appeared.

Acknowledgements This work was supported by the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement n° 261752, PLANTFOODSEC “Plant and Food Biosecurity, Network of Excellence”.

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