DOI 10.12905/0380.sydowia77-2025-0141 Published online 10 September 2024

Diversity of endophytic fungi in potato (*Solanum tuberosum*) plants in Iran

Nasim Alijani Mamaghani

Laboratory of Mycology, Department of Plant Protection, Faculty of Agricultural Sciences Engineering, College of Agriculture and Natural Resources, University of Tehran, Karaj, Iran
Current address: Department of Plant Agriculture, University of Guelph, Ridgetown, ON, Canada

e-mails: nalijani@uoguelph.ca, alijani.nassim@gmail.com

Alijani Mamaghani N. (2024) Diversity of endophytic fungi in potato (*Solanum tuberosum* L.) plants in Iran. – Sydowia 77: 141–147.

The endophytic mycobiota of 84 symptomless mature potato plants collected in 21 farms each of two Iranian provinces, Ardebil and south Kerman, were studied. A total of 491 isolates yielded 52 different fungal taxa. Some of the taxa isolated are known as potato pathogens and a few of them (especially *Fusarium* spp.) potential mycotoxin producers. *Alternaria* spp. were dominant in both sites in the aerial and *Fusarium* spp. in the underground parts. Almost all other taxa were present at frequencies <10 %. The two sites were quite similar with regards to their evenness values, but the species richness of the Kerman samples was higher. The most common endophytic species displayed an organ specificity that allowed distinguishing between aerial and underground organs.

Keywords: biodiversity, ecology, endophyte, organ specificity.

Endophytic fungi are ubiquitous in the plant kingdom (Arnold et al. 2009, Carroll 1988, Petrini 1986, Rodriguez et al. 2009, U'Ren et al. 2019), and their presence has been reported also in lichens (Arnold et al. 2009, Petrini et al. 1992, U'Ren et al. 2019), but still not very much is known about the role of endophytic fungi in the endophyte-host symbiosis. Clavicipitaceous endophytes have been shown to be beneficial to their host plant, enhancing plant resistance against herbivores by producing toxic compounds, or increasing growth, photosynthetic rate and tolerance to biotic and abiotic stresses (Kauppinen et al. 2016), whereas the presence of known pathogens among isolated endophytes has led to the hypothesis that some plant pathogens are latent within their host tissues for a considerable period (Petrini 1991), an assumption later confirmed by other researchers (e.g., Slippers & Wingfield 2007).

The endophytic mycobiota of potato, a major staple food in many countries and the third leading crop of Iran after wheat and maize (Imani et al. 2021), is poorly known. So far, only three studies have dealt with endophytic fungi of *S. tuberosum*. O'Callaghan et al. (2005) studied the microbial communities of magainin-producing transgenic lines of *S. tuberosum* in New Zealand. In Germany, Götz et al. (2006) investigated the fungal endophytes in roots of field-grown transgenic T-4 lysozyme producing potatoes and their parental line by traditional isolation and cultivation- independent DNA-based methods, and Marak & Kayang (2018) isolated and identified the endophytic fungi associated with *S. tuberosum* in India.

This work has been undertaken to determine the biodiversity of endophytic fungi from potato plants collected at two sites in Iran, and to verify whether potato pathogens already reported in potato plants in Iran (Amini et al. 2016; Chehri et al. 2014; Nasr Esfahani 2018a, b, 2020) may be present as endophytes in the Iranian crops.

Materials and methods

Sample collection

Mature, symptomless potato plants were randomly collected in potato fields in the provinces Ardebil (Northwestern Iran) and South Kerman (Southeastern Iran).

The Ardebil province is a major centre of potato production in Iran and enjoys good climatic conditions, with a humid and cold climate. In 2021, potato accounted for 32.7 % of all crop production

(Imani et al. 2021). The Kerman province is the third largest potato producer in Iran (Amarnameh 2018) with about 77 % of the whole Kerman production originating from the Jiroft area, located in the southern part of this province (Mollae et al. 2020). Total potato production in the Kerman province was reported to amount to approx. 0.4 million tons in 2017 (Amarnameh 2018).

At each site, 21 farms growing potato as the main crop were sampled once. The two sites have different climate conditions, therefore potatoes are planted and harvested at different times of the year. Ardebil (in the Northwest) is humid and cold most of the year, and potatoes are planted in spring (around May) and harvested at the end of summer (August). The climate of Kerman (Southeast) is dry and hot; therefore, farmers plant the potatoes in Fall and harvest them at the end of winter (February). The samples were collected in August 2018 in Ardebil and February 2019 in South Kerman, to keep the sampling as homogeneous and similar as possible. The material was stored in paper bags and kept at 4 °C during transportation to the laboratory, where they were kept at 4 °C until processing, which was carried out within three days of sampling.

Surface sterilization, incubation, and isolation

We collected two healthy, symptomless, mature potato plants at each farm for a total of 42 plants for each site. Forty segments for each organ studied (leaves, stems, roots, and tubers) were cut out at random from the plants collected. Surface sterilization, incubation, and isolation were carried out according to Götz et al. (2006) and Alijani Mamaghani et al. (2022, 2024). Before sterilization, roots and stems were cut in pieces approx. 5 cm long, and tubers in slices 3 mm thick, whereas leaves were kept intact. All samples were then washed in running tap water for at least 15 min and immersed first in 70 % ethanol for 2 min, then in 5 % sodium hypochlorite for 5 min, washed in sterile distilled water 3 times for 5 min, and dried between sterile tissues for 15 min.

Subsequently, leaves and tubers were cut into pieces of 5×5 mm; depending on the size and age, stems and roots were cut into pieces 3 mm thick, 5 mm wide, and tubers pieces of 5–10 mm in diam. Sixteen pieces of each organ (eight piece in each plate) and altogether 64 pieces for each plant were plated onto potato dextrose agar (PDA, Merck, Germany), supplemented with a mixture of antibiotics (penicillin G Na 60 mg/l, streptomycin sulphate 80 mg/l, tetracycline HCL 50 mg/l) to suppress bacterial growth, and incubated at 20 °C in the dark for at least one month. Cultures were regularly monitored for fungal growth and any emerging mycelium was transferred by hyphal tip or single spore isolation onto fresh PDA medium. Pure cultures were preserved on filter papers and kept at –20 °C.

Identification

Regardless of the frequency of isolation, all isolates were identified as exactly as possible. When identification by morphological characters only was not possible, molecular sequencing was used. Sterile isolates were not identified and not considered in the statistical analysis.

All cultures were incubated on PDA and kept at 25 °C for one week in darkness and examined daily for sporulation. Sporulating endophytes were identified to genus and, if possible, species level by light microscopy using standard mycological literature.

Alternaria species were identified according to Simmons (2007) and Woudenberg et al. (2013); isolates were inoculated onto Potato Carrot Agar (PCA) (Crous & Cock 2009) and kept under daily fluorescent light/dark cycle of 8/16 h at 22 °C for 5–7 days.

Cephalotrichum species were identified according to Woudenberg et al. 82017).

Fusarium isolates were incubated on PDA (Merck, Germany), and kept at 25 °C for 3–4 weeks (Leslie & Summerell 2006). Carnation Leaf Agar (CLA) plates were used for the study of macroconidia, chlamydospores, and phialides (Crous & Cock 2009). CLA plates were kept under fluorescent and near ultraviolet light/dark cycles of 12/12 h and 23–25 °C for one week up to two months. Microconidia and phialide production was induced on Synthetic Nutrient Agar (SNA) plates (Crous & Cock 2009) incubated in darkness at 25 °C for one week.

Trichoderma and *Clonostachys* isolates were cultured on PDA media and kept under a near ultraviolet light/dark cycle of 12/12 h at 22 °C for 7 days, and identification was carried out according to Harman & Kubicek (2014).

Each taxon, including those that were present at frequencies <5 %, was considered as an Operational Taxonomic Unit (OTU) for statistical analyses.

Molecular genetic identification was used only for *Alternaria, Cephalotrichum, Clonostachys, Fusarium*, and *Trichoderma* isolates. Molecular identification of *Cephalotrichum* spp. was done according to Alijani Mamaghani et al. (2022). Genomic DNA was extracted from colonies grown on PDA at 25 °C for 7–10 days (Zhong & Steffenson 2001),

and the internal transcribed spacer (ITS) regions 1 and 2 including 5.8 S rDNA (ITS), β-tubulin (*tub2*), translation elongation factor 1α (*tef1*), and Large Subunit of rDNA (LSU) genes were partially amplified and sequenced (Alijani Mamaghani et al. 2022).

Molecular genetic identification of *Fusarium, Alternaria, Trichoderma*, and *Clonostachys* isolates was done according to Alijani Mamaghani et al. (2024). DNA extraction was carried out using the Wizard Magnetic DNA Purification System for Food kit (Promega Corporation, Madison, WI), according to the manufacturer's instructions. Multilocus sequencing based on the genes *tef1, tub2* and ITS was used for the identification of *Fusarium* species (Leslie & Summerell 2006). For *Alternaria* species identification, the glyceraldephyde-3-phosphate dehydrogenase (*gapdh*), and calmodulin (*calm*) gene regions were amplified and sequenced (Woudenberg et al. 2013). ITS, *tef1*, and *tub2* were amplified and sequenced to identify *Trichoderma* and *Clonostachys* isolates (Harman & Kubicek 2014).

The sequences were uploaded in BLASTn (National Center for Biotechnology Information, NCBI: https://blast.ncbi.nlm.nih.gov/) and compared with already available sequences for identification.

Pure cultures of selected isolates are deposited at the Mycology Laboratory of the University College of Agriculture and Natural Resources, University of Tehran, Iran; Institute of Microbiology, University of Applied Sciences and Arts of Southern Switzerland; and the Agricultural Biotechnology Research Institute of Iran (ABRI). Additionally, pure cultures of all *Alternaria, Fusarium, Trichoderma*, and *Clonostachys* are deposited at the Institute of Sciences of Food Production, National Research Council (CNR-ISPA), Bari, Italy.

Statistical analysis

Species richness, defined as the number of species in a given sample, and evenness were calculated and mapped graphically to differentiate communities visually (Gauthier & Derome 2021). Whittaker quantile diagrams (Whittaker 1965) displaying relative species richness were also prepared. Percentages of isolations (number of colonized tissue pieces divided by the number of examined tissue pieces and multiplied by 100) for each organ type and provenance were analysed by Multidimensional Scaling (MDS; classical method and L2 dissimilarity) to evaluate similarities among mycobiota from different organs, considering only those taxa that were present at >5 % in any of the samples studied. A sensitivity analysis was also carried out to evaluate the potential effect of rare isolates by carrying out MDS on the complete dataset [all operational taxonomic units (OTU) detected, including the rare ones].

All computations were carried out with Stata version 17 (StataCorp LLC, College Station, Texas, USA), which was used also to prepare graphical displays.

Results

Fifty-two different fungal taxa were isolated from all samples studied, for a total of 142 isolates in Ardebil and 349 in Kerman. Twenty-four (46 %) were recovered at frequencies >5 % of the total number of colonies in at least one organ (Tab. 1). At both sites, *Alternaria* spp. were dominant in the aerial parts (stems and leaves) and *Fusarium* spp. in the underground organs (roots and tubers). Almost all other taxa were present at frequencies <10 % and did not show any clear organ preference.

The Whittaker plots (Fig. 1A, B) show that the two sites are quite similar regarding the evenness values, with comparatively gentle slopes indicating a rather uniform species distribution in all samples. Only tubers at the Ardebil site have a larger number of dominant taxa. The Kerman site (Fig. 1B) is apparently more species-rich, with a more pronounced evenness, but the small sample size investigated in this study does not allow to draw any firm conclusions. No clear clustering can be seen in Fig. 1C, even if the Kerman samples tend to group more closely.

MDS shows a grouping of samples (Fig. 1D) that suggests a strong organ specificity of the endophytes isolated. The Mardia fit measure of 0.9787, with a percentage explained by the first two dimensions of 80 %, is indicative of a good fit of the model to the data. The first dimension (68 % of the total variance) separates the aerial from the subterranean plant organs, whereas the second dimension (only 11 % of the total variance) separates, albeit less clearly, the two sites.

Discussion

This study shows that the most common fungal endophytes of *Solanum tuberosum* display a marked organ specificity, allowing to distinguish at least between aerial and underground organs. This is not surprising, as previous research has already suggested similar patterns for several other host plants (e.g., Moricca et al. 2012, Schulz & Boyle 2005), along the line suggested by Petrini (1991).

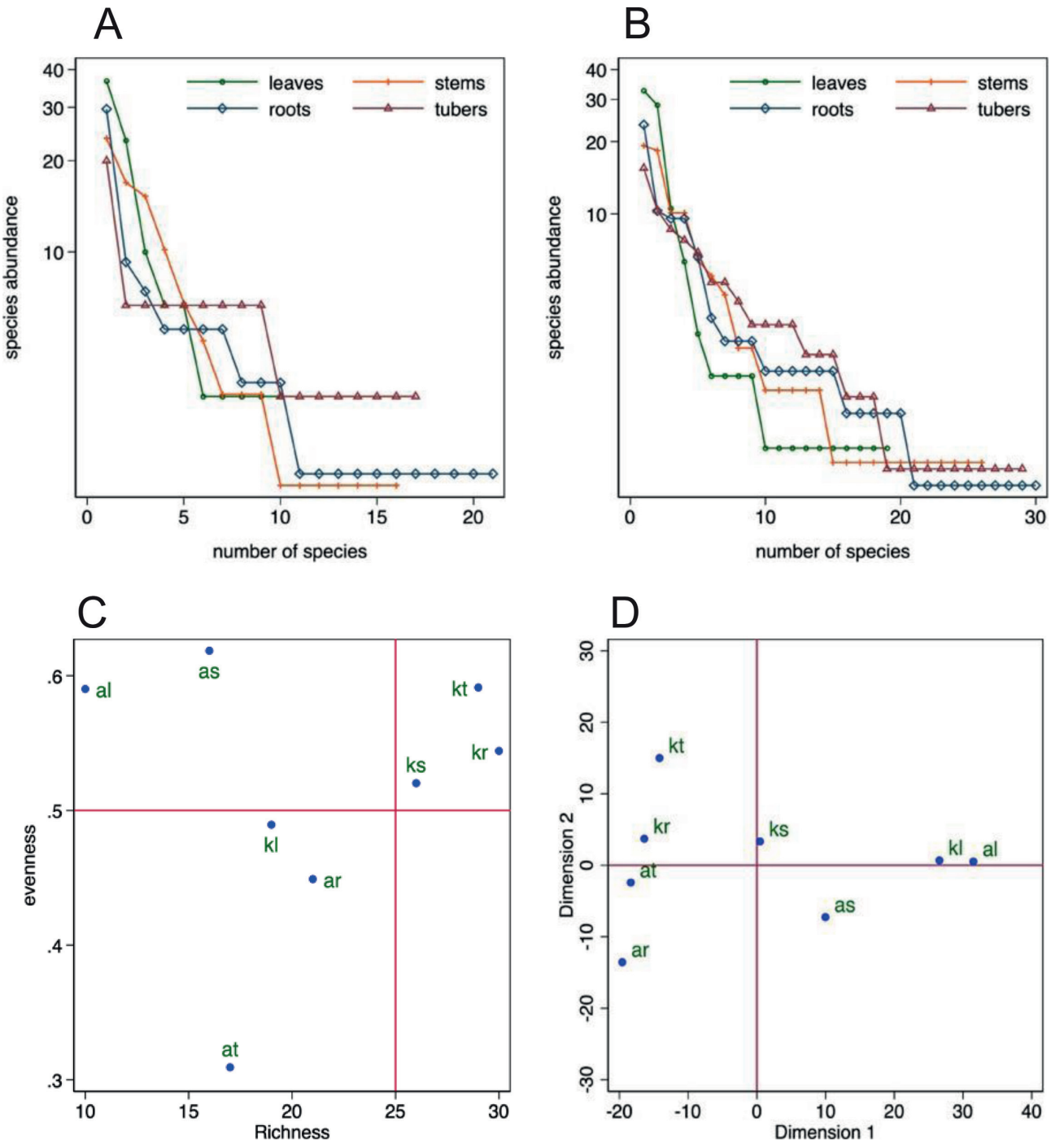

Fig. 1. Analysis of the ecological data collected. **A**, **B**. Whittaker plots, separately by site. **A.** Ardebil. **B.** Kerman. The number of individuals of each OTU are sorted in descending order; the proportion of the total number of individuals for each species is plotted on the log scale against the OTU rank, presenting the richness of each species ranked from the most (rank 1) to the least frequent rank. The plots indicate communities with high dominance by few species. **C**. Plot of the evenness vs. richness data. **D.** Results of the MDS analysis, computed using only OTUs with frequencies >5 %. al: Ardebil, leaf samples; as: Ardebil, stem samples; ar: Ardebil, root samples; at: Ardebil, tuber samples; kl: Kerman, leaf samples; ks: Kerman, stem samples; kr: Kerman, root samples; kt: Kerman, tuber samples.

Tab. 1. Percentage of endophytes species ((number of colonized tissue pieces divided by the number of examined tissue pieces and multiplied by 100) recovered at frequencies >5 % of the total number of colonies in at least one organ (total number of samples studied: 40). A Ardebil; K Kerman. For species authorities see indexfungorum.org.

Taxon	Leaves		Stems		Roots		Tubers	
	A	K	A	K	A	K	A	K
Alternaria								
A. alternata	23.33	28.42	10.17	6.42	–	2.94	–	–
A. arborescens	6.67	1.05	–	0.92	–	–	–	–
A. lini	3.33	1.05	16.95	0.92	–	–	–	–
A. viburni	10.00	–	–	–	1.85	–	–	–
Alternaria sp. 2	36.67	32.63	23.73	18.35	1.85	2.21	–	1.72
Fusarium								
F. equiseti	–	–	3.39	–	7.41	1.47	3.33	–
F. nirenbergiae	–	–	–	–	5.56	2.94	–	2.59
F. nygamai	–	–	–	–	–	6.62	–	5.17
F. oxysporum	–	–	–	1.83	1.85	0.74	6.67	1.72
F. redolens	–	–	–	–	5.56	–	–	–
F. solani	–	–	1.69	–	5.56	2.21	6.67	0.86
Fusarium sp.	3.33	10.53	15.25	19.27	29.63	23.53	20.00	10.34
Aspergillus sp.	–	6.32	1.69	10.09	1.85	9.56	3.33	8.62
Acremonium sp.	–	2.11	5.08	2.75	–	2.94	6.67	6.90
Cephalotrichum gorgonifer	3.33	–	–	–	–	1.47	6.67	3.45
Cladosporium sp.	–	–	–	5.50	–	2.21	–	3.45
Clonostachys rosea	–	1.05	–	0.92	5.56	0.74	6.67	0.86
Colletotrichum sp.	–	–	1.69	0.92	9.26	–	3.33	–
Nigrospora sp.	6.67	–	–	–	–	–	6.67	–
Penicillium sp.	–	1.05	3.39	2.75	3.70	3.68	3.33	7.76
Plectosphaerella sp.	–	–	1.69	0.92	1.85	1.47	6.67	–
Rhizoctonia sp.	–	–	–	–	3.70	10.29	3.33	0.86
Trichoderma harzianum	–	2.11	–	0.92	–	2.21	–	5.17
Verticillium sp.	–	–	6.78	0.92	1.85	–	3.33	2.59

The richness and evenness data (Figs. 1A–C) indicate that comparatively few taxa account for a large percentage of the overall colonisation of each organ. For instance, the six *Alternaria* species isolated from the aerial plant organs at both sites account, on average, for more than 50 % of all isolates (range: 26–80 %), and the seven *Fusarium* spp. for approx. 30 % (range: 18–43 %). *Alternaria* spp. are colonizing mostly aerial, *Fusarium* spp. underground organs, and this distribution heavily influences the results of the MDS analysis.

Pathogenic *Alternaria* species have already been reported from Iran (Amini et al. 2016; Nasr Esfahani 2018a, b). Of the *Alternaria* species known to cause the potato early blight disease (Kokaeva et al. 2017), we were able to detect only *A. alternata* and *A. arborescens* in our samples. An additional *Alternaria* taxon could not be identified with the primers used, but we cannot exclude that *Alternaria* sp. 2 could also belong to the *Alternaria* complex known to cause early blight and brown spot diseases of potato and tomato (Kokaeva et al. 2017).

Fusarium dry rot is a well-known postharvest fungal disease of potato tubers (Bojanowski et al. 2013) that can affect up to 60 % of the tubers and trigger large yield losses (Heltoft et al. 2016). The

disease is caused by several species of *Fusarium* such as, in order of importance, *F. solani* var. *coeruleum*, *F. sambucinum*, *F. oxysporum*, *F. avenaceum*, and *F. culmorum* (Heltoft et al. 2016), and we have detected at least two of them, *F. oxysporum* and *F. solani*, the latter already reported from Iran (Chehri et al. 2014), among our isolates. Several *Fusarium* species are known to produce mycotoxins (Munkvold 2017), and we cannot exclude that some of the species isolated could also be mycotoxin producers (Alijani Mamaghani et al. 2024).

Our study is preliminary in nature and as such has some limitations. First, we were able to collect plants at only two sites, although we tried to capture a reliable biodiversity by collecting plants at 21 separate farms. With the literature available we were not able to identify all isolated taxa to the species level, and the lack of adequate financial means did not allow sequencing of all isolates. Finally, the presence of epiphytic fungi or dormant propagules present on the organ surface and escaping killing by sterilisation among our isolates may have led to false positive results.

These limitations notwithstanding, we could show that selected known potato pathogens are already present in healthy, symptomless plants and may become pathogenic when the ecological conditions are favourable, as convincingly shown by Slippers & Wingfield (2007) for the *Botryosphaeriaceae*.

Acknowledgements

I thank Prof. Orlando Petrini, University of Applied Sciences of Southern Switzerland, for all his support during my PhD and preparation of this paper. Also, the University of Tehran, University of Applied Sciences and Arts of Southern Switzerland (SUPSI), and the Centro Nazionale di Ricerca, Istituto di Scienze delle Produzioni Alimentari (CNR-ISPA), Bari, Italy are acknowledged for allowing me to conduct parts of this research at their facilities. This work was supported by the Iran National Science Foundation (INSF) [grant number 98015699].

References

Alijani Mamaghani N., Masiello M., Somma S., Moretti A., Saremi H., Haidukowski M., Altomare C. (2024) Endophytic *Alternaria* and *Fusarium* species associated to potato plants (*Solanum tuberosum* L.) in Iran and their capability to produce regulated and emerging mycotoxins. *Heliyon* **10**(3). https://doi.org/10.1016/j.heliyon.2024.e26385.

Alijani Mamaghani N., Saremi H., Javan-Nikkhah M., Respinis S.D., Pianta E., Tonolla M. (2022) Endophytic *Cephalotrichum* spp. from *Solanum tuberosum* (potato) in Iran – a polyphasic analysis. *Sydowia* **74**: 287–301. https://doi.org/10.12905/0380

Amarnameh (2018) Statistical Book of Agriculture. 1. Published by Ministry of Agriculture-Jahad, Islamic Republic of Iran. pp. 116. (In Farsi).

Amini J., Sepehrnoosh S., Abdollahzadeh J. (2016).First report of *Alternaria cantlous* causing leaf spot on potato in Iran. *Plant Disease* **100**(3): 653–653. https://doi.org/10.1094/PDIS-08-15-0953-PDN.

Arnold A.E., Miadlikowska J., Higgins K.L., Sarvate S.D., Gugger P., Way A. (2009) A phylogenetic estimation of trophic transition networks for ascomycetous fungi: are lichens cradles of symbiotrophic fungal diversification? *Systematic Biology* **58**(3): 283–97.

Bojanowski A., Avis T.J., Pelletier S., Tweddell R.J. (2013) Management of potato dry rot. Postharvest. *Biology and Technology* **84**: 99–109.

Carroll G. (1988) Fungal endophytes in stems and leaves: from latent pathogen to mutualistic symbiont. *Ecology* **69**(1): 2–9.

Chehri K., Ghasempour H. R., Karimi N. (2014) Molecular phylogenetic and pathogenetic characterization of *Fusarium solani* species complex (FSSC), the cause of dry rot on potato in Iran. *Microbial Pathogenesis* **67–68**: 14–19.

Crous P.W., Cock AWAMd. (2009) Fungal biodiversity: CBS-KNAW Fungal Biodiversity Centre.

Gauthier J., Derome N. (2021) Evenness-richness scatter plots: a visual and insightful representation of shannon entropy measurements for ecological community analysis. *Mphere* **6**(2), 1–10. https://doi.org/10.1128/msphere.01019-20.

Götz M., Nirenberg H., Krause S., Wolters H., Draeger S., Buchner A. (2006) Fungal endophytes in potato roots studied by traditional isolation and cultivation-independent DNA-based methods. *FEMS Microbiology Ecology* **58**(3): 404-413.

Harman G.E., Kubicek C.P. (2014) *Trichoderma* and *Gliocladium*. *CRC Press*.

Heltoft P., Brurberg M.B., Skogen M., Le V.H., Razzaghian J., Hermansen A. (2016) *Fusarium* spp. causing dry rot on potatoes in Norway and development of a Real-Time PCR method for detection of *Fusarium coeruleum*. *Potato Research* **59**(1): 67–80.

Imani B., Allahyari M.S., Bondori A., Emami N., Bilali H.E. (2021) Adoption of organic potato production in Ardabil plain, Iran: an application of the extended theory of planned behaviour. *Potato Research* **64**(2):177–195.

Kauppinen M., Saikkonen K., Helander M., Pirttilä A.M., Wäli P.R. (2016). *Epichloë* grass endophytes in sustainable agriculture. *Nature Plants* **2**(2): Article 2. https://doi.org/10.1038/nplants.2015.224

Kokaeva L.Y., Belosokhov A.F., Doeva L.Y., Skolotneva E.S., Elansky S.N. (2017) Distribution of *Alternaria* species on blighted potato and tomato leaves in Russia. *Journal of Plant Diseases and Protection* **125**(2): 205–212.

Leslie J.F., Summerell B.A. (2006) The *Fusarium* laboratory manual. 1st edn. Blackwell.

Marak M.C.N., Kayang H. (2018) Isolation and identification of endophytic fungi associated with *Solanum tuberosum* L. of south-west Garo Hills, Meghalaya. *International Journal of Advances in Agricultural Science and Technology* **5**(1): 58–65.

Margalef R. (1958) Information theory in ecology. *General Systems* **3**: 36–71.

Mollae A., Hosseinipour A., Azadvar M., Massumi H., Ebrahimi F. (2020) Phylotype and sequevar determination and AFLP fingerprinting of *Ralstonia solanacearum* strains causing bacterial wilt of potato in southeastern Iran. *European Journal of Plant Pathology* **157**(2): 389–402.

Moricca S., Ginetti B., Ragazzi A. (2012) Species- and organ-specificity in endophytes colonizing healthy and declining Mediterranean oaks. *Phytopathologia Mediterranea* **51**(3): 587–598.

Munkvold G. (2017) *Fusarium* species and their associated mycotoxins. In Moretti A., Susca A., (eds.) Mycotoxigenic fungi: methods and protocols. *Methods in Molecular Biology* **1542**: 51–106. Humana Press, New York.

Nasr Esfahani M. (2018a) Analysis of virulence and genetic variability of *Alternaria alternata* associated with leaf spot disease in potato plants in Iran. *Acta Mycologica* **53**(1): 1–9.

Nasr Esfahani M. (2018b) Identification of *Ulocladium atrum* causing potato leaf blight in Iran. *Phytopathologia Mediterranea* **57**: 112–114.

Nasr Esfahani M. (2020) Genetic variability and virulence of some Iranian *Rhizoctonia solani* isolates associated with stem canker and black scurf of potato (*Solanum tuberosum* L.). *Journal of Plant Protection Research* **60**: 21–30.

O'Callaghan M., Gerard E.M., Waipara N.W., Young S.D., Glare T.R., Barrell P.J. Conner A.J. (2005) Microbial communities of *Solanum tuberosum* and magainin-producing transgenic lines. *Plant and Soil* **266**(1–2): 47–56.

Petrini O. (1986) Taxonomy of endophytic fungi of aerial plant tissues. In Fokkema N.J., van den Huevel J., (eds.) *Microbiology of the phyllosphere*. Cambridge, UK: Cambridge University Press: 175–87.

Petrini O. (1991) Fungal endophytes of tree leaves. In Andrews J.H., Hirano S.S., (eds.) *Microbial Ecology of Leaves*, Springer: 179–197.

Petrini O., Fisher P., Petrini L.E. (1992) Fungal endophytes of bracken (*Pteridium aquilinum*), with some reflections on their use in biological control. *Sydowia* **44**: 282–293.

Rodriguez R.J., White Jr J.F., Arnold A.E., Redman R.S. (2009) Fungal endophytes: diversity and functional roles. *New Phytologist* **182**(2): 314–330.

Schulz B., Boyle C. (2005) The endophytic continuum. *Mycological Research* **109**(6): 661–686.

Simmons E.G. (2007) *Alternaria*—An identification manual. American Society of Microbiology.

Slippers B., Wingfield M.J. (2007) Botryosphaeriaceae as endophytes and latent pathogens of woody plants: diversity, ecology and impact. *Fungal Biology Reviews* **21**(2–3): 90–106.

U'Ren J.M., Lutzoni F., Miadlikowska J., Zimmerman N.B., Carbone I., May G., Arnold A.E. (2019) Host availability drives distributions of fungal endophytes in the imperilled boreal realm. *Nature Ecology & Evolution* **3**(10): 1430–1437.

Whittaker R. (1965) Dominance and diversity in land plant communities. *Science* **147**(3655):
250–260.

Woudenberg J.H., Groenewald J.Z., Binder M., Crous P.W. (2013) *Alternaria* redefined. *Studies in Mycology* **75**(1): 171–212.

Woudenberg J.H.C., Sandoval-Denis M., Houbraken J., Seifert K.A., Samson R.A. (2017) *Cephalotrichum* and related synnematous fungi with notes on species from the built environment. *Studies in Mycology* **88**: 137–159.

Zhong S., Steffenson B.J. (2001) Virulence and molecular diversity in *Cochliobolus sativus*. *Phytopathology* **91**(5): 469–476.

(Manuscript accepted 1 August 2024; Corresponding Editor: I. Krisai-Greilhuber)