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Review

Emerging and re-emerging fungus and oomycete soil-borne plant diseases in Italy

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Summary. A disease is recognized as emerging if it is new, it occurs in a new host, there is an unexpected outbreak, its economic importance increases, if it attracts public opinion and the scientific community regardless of economic importance, or if it appears in an area for the first time (referred to as geographic emergence). This review deals with major driving factors of the emergence of plant diseases caused by soil-borne fungi and oomycetes (here indicated as “fungi”), in Italy during recent years. These factors include: accidental introduction of alien pathogens by human activities; effect of climate change; unusually severe weather events; favourable environmental and ecological conditions; pathogen genetic variation; host shifts and expansion of host ranges; introduction or expansion of the geographic range of a susceptible plant species or variety; limited availability of fungicides or development of fungicide-resistance pathogen strains; changes of cropping systems; and/or increased pathogen in soil as a consequence of intensive monoculture of crops. Although in most cases more than a single driving factor contributes to the emergence of an infectious disease, there are examples where a determinant may prevail over others. The case studies reviewed include pathogens belonging to major genera of soil-inhabiting fungi and oomycetes, including *Armillaria*, *Calonectria*, *Coniella*, *Fusarium sensu lato*, *Ilyonectria*, *Monosporoascus*, *Plectosphaerella*, *Rhizoctonia*, *Rosellinia*, *Sclerotinia*, *Sclerotium*, *Verticillium*, *Pythium* and *Phytophthora*. The examples encompass natural and forest ecosystems, economically important agricultural crops including citrus, fruit trees, olive, legumes, vegetables, and ornamentals, as well as exotic or expanding minor crops, such as avocado, goji berry, and pomegranate. Whatever the prevailing driving factor(s) these case studies all show that the large-scale emergence of soil-borne fungal diseases of plants is the consequence of human activities.

Keywords. Exotic pathogens, endemic pathogens, agricultural crops, minor crops, forest ecosystems.

INTRODUCTION

There are different definitions of the term soil-borne when referring to plant pathogens. According to Koike *et al.* (2003), this includes pathogens that infect the plant through the soil while Katan (2017) broadened the con-

cept and defined as soil-borne those pathogens surviving and acting in the soil, at least during part of their lives. Major genera of fungi and oomycetes (Chromista) recognized as typical soil-borne plant pathogens include *Armillaria*, *Fusarium sensu lato* (including *Neocosmospora* spp., formerly the species complex *Fusarium solani*, and other *Fusarium*-like genera recently segregated from *Fusarium sensu lato*), *Gaeumannomyces*, *Macrophomina*, *Cylindrocarpon*-like asexual morphs, *Monosporascus*, *Phytophthora*, *Phytophthium*, *Plectosphaerella*, *Pyrenochaeta*, *Pythium*, *Rhizoctonia*, *Rosellinia*, *Sclerotinia*, *Sclerotium*, *Thielaviopsis* and *Verticillium*. These pathogens are well-studied because of their widespread occurrence in many important world food and fibre crops. However, other genera of plant pathogens, such as *Colletotrichum* as causal agents of anthracnose of many host plants, include species living in soil and affecting important crops (Gilardi *et al.*, 2014c). Whatever the definition, soil-borne fungal pathogens have the following characteristics: they have adapted to living in terrestrial habitats; they infect plants through belowground organs but are also able to cause infections of aboveground parts of the plants; they are saprobic, hemibiotrophic or parasitic on roots, stems and/or leaves of herbaceous or woody plants; and they cause monocyclic, in some cases polyetic and, more rarely, polycyclic diseases.

Soil-borne pathogens causing polycyclic leaf diseases have been frequently reported in Italy in nurseries of ornamentals, as consequences of conducive environments. They include *Calonectria* (Saracchi *et al.*, 2008; Vitale *et al.*, 2013) and *Phytophthora* species (Pane *et al.*, 2007a; Cacciola *et al.*, 2011b; Ginetti *et al.*, 2014). Microsclerotia of *Calonectria* species are the primary inocula and the survival form of these pathogens in the soil, while aerial dissemination occurs through conidia of their *Cylindrocladium*-like anamorphic stage and ascospores. As far as *Phytophthora* is concerned, few species, like *P. infestans*, have adapted to almost completely aerial lifestyles, while the majority of *Phytophthora* species are typically terricolous. A number of species that produce deciduous sporangia have partially adapted to aerial lifestyles (Jung *et al.*, 2018). *Phytophthora palmivora*, in particular, has developed evolutive transitional dispersal conidium-like propagules (sporocysts). Sporocysts are non-papillate caducous sporangia that can be easily detached and dispersed by rain.

A second aspect to be defined is when an infectious disease can be considered to be emerging. In this review, we recognize diseases as “emerging” when they are new, occurring in an area for the first time (geographic emergence), if they occur in new hosts, if there is an unexpected outbreak, if their economic importance increas-

es, or if for some reason they attract public or scientific attention.

In recent years there has been considerable increase in the number of new *Phytophthora* species discovered. The number of validly described and recognized species has increased from approx. 40 in 1990 to 101 by 2011 (Kroon *et al.*, 2011) and now exceeds 150 (Ruano-Rosa *et al.*, 2018b, Albuquerque Alves *et al.*, 2019). The increase in the number of newly described *Phytophthora* species probably results from the scientific interest for these Oomycetes, their spread through the nursery plant trade and the rapid progress and evolution of molecular diagnostic techniques and taxonomy (Cooke *et al.*, 2007; Lamour *et al.*, 2007; Blair *et al.*, 2008; Martin *et al.*, 2012; Scibetta *et al.*, 2012; Bilodeau *et al.*, 2014; Jung *et al.*, 2016a; Yang *et al.*, 2017).

Molecular studies have also revealed the complexity of *Fusarium*, which encompasses numerous soil-borne pathogens of economically important crops. The taxonomy of this genus has undergone substantial revision and numerous new cryptic species have been described which differ in subtle morphological details and were previously assigned to the species complexes of *F. fujikuroi*, *F. incarnatum-equiseti*, *F. oxysporum*, *F. sambucinum* and *F. solani*. These have been separated or reallocated in the genus *Neocosmospora* on the basis of multi-locus phylogenetic analyses (O'Donnell *et al.*, 2015; Schroers *et al.*, 2016; Sandoval-Denis and Crous, 2018; Sandoval-Denis *et al.*, 2018; Lombard *et al.*, 2019; Maryani *et al.*, 2019).

Major determinants of the emergence of infectious plant diseases have been reviewed elsewhere (Fisher *et al.*, 2012; Gonthier and Garbelotto, 2011; Santini *et al.*, 2013; Gilardi *et al.*, 2018a,b; Moricca *et al.*, 2018). These determinants include anthropogenic introduction of alien pathogens, climate change, severe weather events, favourable environmental and ecological conditions, pathogen genetic recombination or mutation, host shifts or expansion of host range, introduction or expansion of the geographic ranges of susceptible plant species or varieties, limited availability of fungicides and development of resistance, changes of cropping systems, and increases in soil inoculum consequences of monoculture. These factors may be involved individually or together, instantaneously or continuously, simultaneously or in succession.

There is a body of direct or circumstantial evidence indicating that emergence of infectious plant diseases results from human activities (Andjic *et al.*, 2011; Mammella *et al.*, 2013; Santini *et al.*, 2013; Barnes *et al.*, 2014; Biasi *et al.*, 2016; Engelbrecht *et al.*, 2017), and several driving factors usually concur to cause emergence of a

disease (Desprez-Loustau *et al.*, 2010; Stenlid *et al.*, 2011; Garbelotto and Pautasso, 2012). The recent study by Serrano *et al.* (2019), of the genetic structure of *P. cinnamomi* isolates of worldwide origin, using four micro-satellite markers, showed that identical genotypes of this pathogen were associated with the same hosts on different continents. This indicated long-distance transport by man, while the presence of identical genotypes in agricultural settings and neighbouring wildlands would suggest that specific commodities may have been the common sources of recent infestations caused by new invasive genotypes.

The present review considers emerging soil-borne plant diseases reported in Italy during recent years. These examples exemplify prominent roles of disease emergence drivers.

INTRODUCTION OF ALIEN PATHOGENS

In the modern era, the most devastating plant disease epidemics have been caused by exotic invasive pathogens. The causal agents of several devastating *Phytophthora* epidemics in Europe, Australia, and North America, including those caused by *P. ×cambivora*, *P. cinnamomi*, *P. lateralis*, *P. plurivora* and *P. ramorum*, have probably originated in South-east Asia (Jung *et al.*, 2016a; Jung *et al.*, 2018). Intensification of international trade of plant material and increased efficiency and speed of transport have favoured the introduction of pathogens into new areas. Most alien emerging pathogens have been inadvertently introduced with exotic plants or imported plant materials. Seeds and timber can be vectors of soilborne plant pathogens, but the nursery trade has been increasingly identified as responsible for the movement of this group of pathogens, despite phytosanitary regulations of international trade of plants and commodities (Migliorini *et al.*, 2015; Jung *et al.*, 2016b; Simamora *et al.*, 2017; Jung *et al.*, 2019). During visual inspections, soil-borne pathogens often go undetected because they induce obvious symptoms only in advanced stages of infection. The most commonly moved soil-borne pathogens globally are species of *Phytophthora* (Brasier, 2008). Genetic analysis of the variability of large numbers of isolates of the cosmopolitan and polyphagous plant pathogen *P. nicotianae*, from a wide range of geographic origins and hosts including ornamentals and agricultural crops, revealed that isolates from *Citrus* spp. were genetically related. This was regardless of their geographic origin, and these pathogens were characterized by genetic uniformity and high inbreeding coefficients (Mammella *et al.*, 2013; Biasi *et*

al., 2016). Greater variability was observed for populations from other hosts and a significant geographical structuring was found only for isolates from *Nicotiana* and *Solanum* spp. These differences were possibly related to the propagation systems for different crops. Isolates obtained from *Citrus* spp. are more probably distributed worldwide with infected nursery plants, whereas *Nicotiana* and *Solanum* spp. are propagated by seeds, which would not contribute to the spread of the pathogen and result in a greater opportunity for geographic isolation of different lineages. For ornamental species in nurseries, the high genetic variation is likely to result from mixtures of diverse pathogen genotypes through the trade of infected plant material from various geographic origins, the presence of several host plants in the same nursery, and genetic recombination through sexual reproduction of this heterothallic pathogen (Mammella *et al.*, 2013; Biasi *et al.*, 2016).

Restoration plantings or afforestation with nursery plants are pathways for the introduction and spread of exotic *Phytophthora* species in natural habitats and forests (Sims *et al.*, 2019a, b). In a recent survey of protected natural areas and water courses crossing these areas in Sicily, 13 of 20 recovered *Phytophthora* species were exotic, while only seven, including *P. tyrrhenica* and *P. vulcanica* associated with *Fagaceae* hosts, could be regarded as endemic to Europe (Jung *et al.*, 2017; Jung *et al.*, 2019). Several species found in this survey, including *P. cactorum*, *P. citrophthora*, *P. megasperma*, *P. multivora*, *P. plurivora* and *P. ×cambivora*, are well-known invasive pathogens with wide host ranges and aggressiveness towards many cultivated and native European plant species. The presence of these pathogens indicates that they constitute threats to the homeostasis and resilience of these ecosystems, and protected natural areas are reservoirs of inoculum of potential pathogens for economically important crops. Garbelotto and Hayden (2012) highlighted the link between the ornamental plant industry and the introduction of *P. ramorum*, which causes lethal cankers on oak species native to California, into the wildlands in North America. *Phytophthora ramorum* is a quarantine pathogen also in the EPPO region (in the A2 list from 2013), has been repeatedly intercepted in nurseries of ornamentals in Italy, but was promptly eradicated (Ginetti *et al.*, 2014). It has also been detected as an operational taxonomic unit (OTU) by metabarcoding analyses of soil samples sourced from chestnut stands in central Italy and ornamental nurseries in southern Italy (Vannini *et al.*, 2013; Prigigallo *et al.*, 2016). However, in both cases, the presence of the pathogen in samples was not confirmed by the isolation of living cultures. The official status of *P.*

ramorum in Italy, based on information updated to 2014, is “transient, under eradication”. *Phytophthora niederhauserii*, another invasive polyphagous species, has recently emerged in many countries (Abad *et al.*, 2014). The occurrence of this species in natural ecosystems in Australia, in vineyards (*Vitis vinifera*) in South Africa and in almond (*Prunus dulcis*) trees in California, Spain and Turkey, and its capability to infect shrubs and herbaceous ornamentals in several unrelated families indicates *P. niederhauserii* has wide ecological adaptability and may threaten agricultural and natural ecosystems. There is evidence indicating that after the first detections of *P. niederhauserii* in Italy (Brasier, 2008; Cacciola *et al.*, 2009 a, b), this species has been spreading in nurseries of ornamental plants (Faedda *et al.*, 2013a; Prigigallo *et al.*, 2015; Aiello *et al.*, 2018). *Phytophthora tentaculata* is another emerging but less invasive, exotic *Phytophthora* species that has been reported in northern Italy and on origanum (*Origanum vulgare*) and on loof chicory (*Cichorium intibus*) in central Italy (Martini *et al.*, 2009; Garibaldi *et al.*, 2010). *Phytophthora capsici* remains a serious and economically important pathogen on bell pepper, tomato, eggplant and cucurbits in many countries. This pathogen occurs in protected crops and in open fields, causing severe losses (Hausbeck and Lamour, 2004). The type culture of *P. capsici* is from Italy and was deposited in 1927, suggesting this species was introduced into this country in the 20th century. The long-standing presence of *P. capsici* in Italy is reflected by high levels of genetic variability of the Italian population of this pathogen but its centre of origin remains unknown (Quesada-Ocampo *et al.*, 2011).

Fusarium oxysporum f. sp. *radicis-cucumerinum*, which causes wilting, root and stem rots on cucumber, was first observed in Greece and then in Spain in 2001 and Turkey in 2009, and has been recently reported in Italy on farms that have repeatedly grown cucumber in the same soil for 10 years (Garibaldi *et al.*, 2016). This pathogen can also infect other cucurbit crops, including melon (*Cucumis melo*), watermelon (*Citrullus lanatus*) and sponge gourd (*Luffa aegyptiaca*), while the interspecific hybrids of *Cucurbita maxima* × *C. moschata* and zucchini are not susceptible (Vakalounakis *et al.*, 2005).

Fusarium solani f. sp. *cucurbitae* is responsible for severe losses, causing root and stem rots, particularly on cucumbers in greenhouses. This pathogen is spreading in Spain, where it was reported for the first time in Europe (Gómez *et al.*, 2014). Significant economic damage caused by this pathogen can be expected in Italy in intensive cultivation systems as it can be transmitted by seeds (Vannacci, 1980), and has several cucurbit hosts, including *Cucurbita* hybrids (*C. maxima* × *C. moscha-*

ta) used as rootstocks for watermelon (Armengol *et al.*, 2008).

Fusarium wilt of lettuce (*Lactuca sativa*) caused by *F. oxysporum* f. sp. *lactucae* has recently become the most important disease of lettuce in cultivation areas in many countries, and its spread is favoured by seed transmission (Cabral *et al.*, 2018). Until recently, three races of *F. oxysporum* f. sp. *lactucae* were described and reported: race 1 in Europe, USA and South America and races 2 and 3 in Japan. However, in 2017, a new race, race 4, was detected in the Netherlands, identified through biological assays and molecular tools (Gilardi *et al.*, 2017). This new race is apparently spreading rapidly and has been observed in several European countries, including Belgium, the United Kingdom, Ireland (Taylor *et al.*, 2019) and Italy (Gilardi *et al.*, 2019). The presence of this new race is posing serious threats to growers and plant breeders. Before resistant varieties can be developed, preventative management measures, such as the use of healthy seeds and/or seed treatments, are required to reduce the risk of its rapid spread to new areas. Gilardi *et al.* (2017) speculated that race 4 may have evolved due to high selection pressure as a consequence of lettuce monoculture, or could have been introduced from a foreign source through infected seeds or seedlings.

Careful monitoring of the race situation in the field would be useful for the efficient use of host resistance for disease management. Specific molecular markers can also provide successful detection and identification of *formae speciales* and races of *F. oxysporum* from seeds, plants, and soil samples.

Three vegetative compatibility groups (VCGs), VCG-300, VCG-301 and VCG-302, corresponding, respectively, to races 1, 2 and 3, have been reported in *F. oxysporum* f. sp. *lactucae* (Pintore *et al.*, 2017). The Arizona, California and type 1 isolates from Taiwan all belong to the same VCG as race 1 isolates from Japan, and all the race 1 isolates from Arizona, California and Japan have identical mtSSU and EF-1 α sequences and almost identical intergenic spacer (IGS) region sequences. This indicates a common origin of the three races. However, the possibilities of the pathogen being introduced from a foreign source through infected seeds or seedlings, or of evolution from non-pathogenic *F. oxysporum*, cannot be excluded. The isolates obtained from lettuce in the Netherlands belong to VCG-303 (Pintore *et al.*, 2017). Further studies are needed to elucidate why and how a new race of this pathogen has developed in Northern Europe.

Melon collapse, commonly considered a synonymous of Monosporascus root rot of melon and vine decline (MRRVD), one of the most important disease of melon and watermelon (Martyn and Miller, 1996;

Cohen *et al.*, 2000), has emerged in the last 15 years in Italy. The exotic Ascomycete *Monosporascus cannonballus* has been regarded as the main cause of the disease in several countries (Stanghellini *et al.*, 2003; Chilosi *et al.*, 2008). However, lines of evidence indicate that other soilborne pathogens, such as *Acremonium cucurbitacearum*, the most common fungal species associated to this disease in Spain (García-Jiménez *et al.*, 2000), *Olpidium* and *Plectosphaerella* species, *Macrophomina phaseolina* and *Rhizoctonia* species, are also involved in melon collapse (Bruton, 2000; García-Jiménez *et al.*, 2000; Stanghellini *et al.*, 2010; Stanghellini and Misaghi 2011; Ben Salem *et al.*, 2013; Felipe *et al.*, 2018). Recently in central Italy, *M. cannonballus*, *O. bornovanus*, and *O. virulentum* were recovered from a melon greenhouse soil with a history of severe infections of *Melon necrotic spot virus* (MNSV), which is vectored by *Olpidium* spp. In pathogenicity tests, all three fungi induced symptoms of root rot and vine decline, confirming a complex aetiology of MRRDV (Aleandri *et al.*, 2017). A binucleate *Rhizoctonia* AG-F was reported to be responsible for watermelon vine decline in Sicily (Aiello *et al.*, 2012). Carlucci *et al.* (2012) found several species of *Plectosphaerella* associated with melon collapse in southern Italy, including an already known species, *Pa. cucumerina* (= *Plectosporum tabacinum*), along with four new species, *Pa. citrullae*, *Pa. pauciseptata*, *Pa. plurivora* and *Pa. ramiseptata*. Carlucci *et al.* (2012) also showed that *A. cucurbitacearum* was a synonym of *Nodulisporium melonis*, and transferred it to the genus *Plectosphaerella* as *Plectosphaerella melonis* comb. nov. This increased to six the number of *Plectosphaerella* species reported on melon and watermelon in Italy. However, the roles of new *Plectosphaerella* species in MRRVD have not yet been clarified (Carlucci *et al.*, 2012). Some were reported to be responsible for root rot of other vegetable crops such as tomato, pepper, parsley and basil (Raimondo and Carlucci, 2018a and b). *Monosporascus cannonballus* has been found only on *Cucurbitaceae*, commonly in arid, hot climates (Stanghellini *et al.*, 1996). This pathogen is widespread in major melon-producing countries in North and Central America, Asia, North Africa, and Europe (Martyn and Miller, 1996; Cohen *et al.*, 2000). After the phase-out of methyl bromide fumigation and application of fungicides through irrigation systems, crop rotation with non-susceptible host plants, breeding for disease resistance and grafting on resistant rootstocks have been regarded as alternatives for the management of melon vine decline (Cohen *et al.*, 2000). Grafting on resistant rootstocks is an effective means for the management of a number of soil-borne diseases of veg-

etables (Cohen *et al.*, 2007; Davis *et al.*, 2008), and is increasingly used in Italy in commercial *Solanum* and cucurbit crops (Gilardi *et al.*, 2011; Colla *et al.*, 2012; Gilardi *et al.*, 2014a, b, c). However, no commercial rootstocks of melon and watermelon combine multiple resistance to melon collapse and Fusarium wilt with good production performance (Gilardi *et al.*, 2013).

CLIMATE CHANGE AND SEVERE WEATHER EVENTS

The role of climate change in the emergence of infectious plant diseases, its impact on endemic plant pathogens and the interactions between climate change and the introduction of exotic pathogens as a result of globalization have been the subjects of study and extended debate within the international scientific community (La Porta *et al.*, 2008; Pautasso *et al.*, 2012; Ramsfield *et al.*, 2016; Gilardi *et al.*, 2018b). Several studies have concerned effects of climate change on soil microbial communities and, in particular, on soil-borne pathogens (Dukes *et al.*, 2009; Manici *et al.*, 2014; Kubiak *et al.*, 2017; Gilardi *et al.*, 2018a). Climate change can have direct and indirect effects on plant disease epidemics, as climate affects host susceptibility, the survival of pathogen inoculum, the rate of disease progress and epidemic duration. Frequencies of extreme climatic conditions, such as droughts, floods and hurricanes, as well as damage caused by wind, snow and hail, are also likely to increase due to climate change (IPCC, 2019). According to projections, the increase in temperatures will favour expansion of the geographical ranges of mesophilic and thermophilic pathogens at their northern limits in the Northern hemisphere. More generally, warming is expected to cause pole-ward range shifts of plants and their pathogens affecting natural and managed ecosystems (Chakabortry, 2013).

Jung (2009) imputed the decline of European beech (*Fagus sylvatica* L.) in Central Europe to the interaction between *Phytophthora* spp. infections and climatic extremes. On the basis of a survey of natural parks and reserves in Sicily, it has been assumed that the interaction between climate change and root infections by *P. × cambivora* and other less frequent or less aggressive *Phytophthora* species (Jung *et al.*, 2017; Jung *et al.*, 2019) is the main driving factor of the decline of European beech in the Nebrodi regional park (Sicily, southern Italy). This is the extreme southern limit of the natural geographical range of European beech in Europe. *Phytophthora × cambivora* is also the prevalent species responsible for the resurgence of ink disease in central Italy. Although the effects of climate change on the complex interac-

tions between the diverse components of pathobiomes in agricultural and natural ecosystems are not fully known, there is abundant literature predicting altered geographic distribution of pathogens with changing climate suitability and host distribution (Shaw and Osborne, 2011). For example, a model for predicting the global distribution of *P. cinnamomi*, which is a generalist soil-borne pathogen with a very wide host range, has been developed. This pathogen is considered one of the 100 worst invasive alien species in many countries (Hardham and Blackman, 2018). Since it was first detected on avocado (*Persea americana*) (Cacciola *et al.*, 1998), the number of records of this pathogen in Italian ornamental and forest nurseries, agricultural crops, plantation forests and native woodlands has been increasing (Scanu *et al.*, 2013; Pilotti *et al.*, 2014; Frisullo *et al.*, 2018; Vitale *et al.*, 2019). The model is based on the response of the pathogen to temperature and moisture, and incorporates extensive empirical evidence on the presence of *P. cinnamomi* in the soil (Burgess *et al.*, 2017). Consistently with the model, the comprehensive global map of the *P. cinnamomi* distribution also includes Italian regions with temperate climates, where *P. cinnamomi* has been recently reported as the main stressor threatening the forest stands of evergreen Mediterranean oaks and the Mediterranean maquis vegetation (Scanu *et al.*, 2015; Moricca *et al.*, 2016; Frisullo *et al.*, 2018). A study of diversity and distribution of *Phytophthora* species in chestnut (*Castanea sativa*) stands, and their association with ink disease in Europe, showed that *P. cinnamomi* had peculiar ecological requirements compared to the other species occurring in the chestnut rhizosphere (Vettraino *et al.*, 2005). The pathogen was never detected from sites characterized by minimum and maximum temperatures, respectively, below 1.4°C and above 28°C. This confirms that climate change is a major driving factor conditioning the geographical distribution and emergence of this pathogen that is inhibited by low soil temperature. The rise in temperatures as a result of climate change, along with other factors, may have favoured the emergence of *Pythium* root rot caused by thermophilic *Pythium* species, in leafy vegetables crops in Northern and Southern Italy (Garibaldi *et al.*, 2010; Garibaldi *et al.*, 2015; Gilardi *et al.*, 2018c).

The combined effects of temperature and atmospheric CO₂ concentration on the severity of infections by fungal pathogens in vegetable crops, including the soil-borne pathogen *F. oxysporum*, has been tested in controlled environment conditions simulating global warming (Ferrocino *et al.*, 2013; Chitarra *et al.*, 2015; Gullino *et al.*, 2018). The information provided by these experiments can be useful for developing provisional models

to forecast and counteract the effects of climate change on plant diseases caused by soil-borne pathogens.

A consequence of climate change is the increase in the frequency, extent, and intensity of extreme weather events, although these events are not necessarily linked to global warming. Climate change is believed to be responsible for the increasing frequency of medicanes, which are hurricanes of the tropical type occurring in the Mediterranean Sea. Extreme, severe weather events may trigger the emergence of soil-borne plant diseases as they predispose host plants to the infections and favour pathogen spread. The resurgence of mal secco disease (caused by *Plenodomus tracheiphilus*) in lemon (*Citrus ×limon*) orchards in the Syracuse province during the last few years may be imputed to severe hailstorms and the high susceptibility of 'Femminello Siracusano 2Kr' (Migheli *et al.*, 2009). This is the prevalent cultivar in new plantings of this typical lemon growing area of Sicily. Medicanes were the drivers of epidemic outbreaks of citrus fruit brown rot and foliage blight in Sicily, caused by *P. citrophthora* (De Patrizzio *et al.*, 2012). This is a common soil-borne pathogen which has adapted to an occasional aerial lifestyle.

ENVIRONMENTAL AND ECOLOGICAL CONDITIONS

Environmental and ecological conditions, including warm temperatures, high relative humidity and conducive soil conditions, such as low pH, presence of residues of previous susceptible crops and overwatering, may be major drivers of the emergence of diseases caused by polyphagous soil-borne pathogens. The following case studies illustrate these interactions.

Damping-off, caused by *Pythium ultimum*, has been observed with increasing frequency in Italy on lettuce, wild rocket and lamb's lettuce at temperatures between 15 and 25°C (Gilardi *et al.*, 2018a, b). *Pythium ultimum* has also been reported in northern Italy on coriander (*Coriandrum sativum*) for the first time in the world (Garibaldi *et al.*, 2010a). The presence of new species of *Pythium* in Italy, such as *P. aphanidermatum* on spinach and on swiss chard, *P. irregulare* on lamb's lettuce and *Pythium* Cluster B2a (*P. dissotocum*, *P. coloratum*, *P. diclinum*, *P. dictyosporum*, *P. lutarium*, *P. sp.* 'Group F' and *P. sp. tumidum*) on lettuce is particularly important at warm temperatures (Garibaldi *et al.*, 2015d; Gilardi *et al.*, 2018b, c). Web blight and damping-off of seedlings, caused by the *Rhizoctonia solani* complex, have recently been found on many hosts of different families, including species of *Campanula* (*C. trachelium*, *C. rapunculodes* and *C. carpatica*), *Rebutia perplexa*, *Nigella dama-*

scena, *Lavandula officinalis*, *Origanum vulgare*, *L. stoechas*, *Rosmarinus officinalis*, *Satureja montana*, *Dodonea viscosa*, *Coprosma repens* and *C. lucida*, *Viburnum tinus*, *Murraya paniculata*, *Streptosolen jamesonii*, *Thyptomene saxicola*, *Chamaerops humilis*, *Passiflora mollissima* and *Tabebuia impetiginosa* (Garibaldi *et al.*, 2015a, c, e, g; Bertetti *et al.*, 2017; Aiello *et al.*, 2017b; Bertetti *et al.*, 2018a,b). Southern blight caused by *Sclerotium rolfsii* (teleomorph *Athelia rolfsii*) has been reported on numerous host plants grown either in pots or in fields, in greenhouses or in the open air, in northern and southern Italy. These host include *Dichondra repens*, potato, common bean, *Stevia rebaudiana*, *Hedera helix*, *Cannabis sativa*, ornamental *Citrus* species, *Convolvulus cneorum* and young seedlings of several other ornamental plants (Pane *et al.*, 2007b, c; Polizzi *et al.*, 2007; Pane *et al.*, 2008; Polizzi *et al.*, 2010; Garibaldi *et al.*, 2013). *Sclerotinia sclerotiorum*, a necrotrophic pathogen known to infect over 400 species of plants from 75 families (Grabowski, 2017), has been observed on many aromatic and ornamental plants, such as thyme, sage, borage, mint, rosemary, aquilegia, petunia, paris daisy, lavender, and gaillardia (Garibaldi *et al.*, 2008; Garibaldi *et al.*, 2015b, f; Garibaldi *et al.*, 2017). Several species of *Fusarium*, *Cylindrocarpon*-like asexual morphs (*Ilyonectria*, *Pleiocarpon*) and *Neocosmospora*, have been reported on ornamental plants, including *Agapanthus africanus*, *Bougainvillea glabra*, *Cordyline australis*, *Dasyllirion longissimum*, *Eremophila* spp., *Philotea myoporoides*, *Strelitzia reginae*, *V. tinus* as well as *Trachycarpus princeps* and various other *Arecaceae* species (Aiello *et al.*, 2014; Aiello *et al.*, 2017a; Guarnaccia *et al.*, 2019). Climatic conditions, farming practices, and conducive environmental conditions have been indicated as major drivers of the emergence of these soil-borne pathogens of ornamental plants.

PATHOGEN GENETIC RECOMBINATION OR MUTATION

Successful invasion by an exotic pathogen may depend on its evolutionary potential which allows it to emerge, adapt to new hosts and environments and persist in populations of host plants. It is generally assumed that asexual organisms may exhibit lower invasion success compared to sexually reproducing organisms, due to their inability to generate meiotic progeny which can rapidly adapt to new hosts and environments. Despite, mechanisms generating variation, such as genetic recombination and mutations, are not always associated with fitness benefits. There are several examples showing that

clonality does not necessarily reduce invasiveness (Prospero and Cleary, 2017). One of the best documented cases of genetic recombination of an invasive soil-borne plant pathogen is that of *Heterobasidion irregulare* native to North America. This pathogen was accidentally introduced into Italy, and has become invasive in Latium (central Italy), where the Italian stone pine (*Pinus pinea*) is the sole or major pine species. In this invasion area *H. irregulare* prevails on the native sibling species *H. annosum*, and, unlike *H. annosum*, is also able to colonize as a saprophyte pure oak stands (Gonthier *et al.* 2012; Giordano *et al.* 2013; Garbelotto *et al.* 2013). There is evidence in the invasion area, where *H. irregulare* and *H. annosum* are in sympatry, of interspecific pathogen hybridization and introgression of genes, mostly from the native species into the invasive one, suggesting rapid, possibly adaptive, evolution of *H. irregulare* (Gonthier *et al.* 2007; Linzer *et al.*, 2008; Gonthier *et al.* 2015). Epidemiological consequences of this evolution are unpredictable, and no studies have determined how gene introgression may affect fitness and virulence of either the invasive or the native species. However, examples from other organisms, including several plant pathogens, indicate gene introgression is an important evolutionary mechanism, increasing adaptation and pathogenicity of the species involved (Brasier, 2001; Depotter *et al.*, 2016). Interspecific hybrids of *Phytophthora* occur frequently in natural ecosystems and may become invasive (Brasier *et al.*, 2004; Ioos *et al.*, 2006; Burgess, 2015). Hybridization and polyploidy are assumed to be the genetic mechanisms for adaptation to new hosts and speciation in these oomycetes (Bertier *et al.*, 2013). The interspecific hybrid nature, the mating reproduction system (both A1 and A2 mating types occur in Europe) and the intraspecific variability of *P. ×cambivora* may explain the ability of this heterothallic oomycete to adapt to different environmental conditions, ranging from rainforests of Southeast Asia, where the species probably originated, to temperate deciduous forests of central Europe and Southern Italy (Jung *et al.* 2017). In nurseries of ornamental plants, the sympatric occurrence of diverse *Phytophthora* species from different geographic origins favours genetic recombination through sexual reproduction between species that have evolved separately and have not developed pre-mating barriers. A natural hybrid between *P. nicotianae* and *P. cactorum*, referred to as *P. ×pelgrandis*, was reported in Italy as the causal agent of root rot of potted lavender (*L. stoechas*) plants. This interspecific hybrid showed a unique combination of morphological, biological and ecological characteristics inherited from both parental species, some of which may have epidemiological implications (Faedda *et al.* 2013b).

The frequency of natural *Phytophthora* interspecific hybrids in nurseries is possibly greater than expected from the low number of reports. Hybrids, may go unnoticed as they do not always have distinctive morphological traits. Sequencing of ITS-rDNA regions after PCR amplification with universal primers ITS6 and ITS4, often used for molecular identification of *Phytophthora* species, may fail to discriminate these species from their parents. In many cases, application of diverse molecular techniques is required to ascertain the hybrid nature of the isolates (Faedda *et al.*, 2013b). Very recently a rapid High-Resolution Melting (HRM) diagnostic method has been proposed to distinguish *Phytophthora* hybrids from their parental species (Ratti *et al.* 2019).

The high genetic variability of soil-borne vegetable crop pathogens, such as *Fusarium oxysporum* and *P. capsici*, is a challenge and limits application of genetic resistance for the management of the diseases they cause. Evolution or accidental introduction of new pathogen physiological races have been indicated as possible causes of breakdown of rootstock resistance in grafted *Solanum* or cucurbit plants.

Genetic plasticity of *F. oxysporum* and the problem this poses for farmers and plant breeders are exemplified in *F. oxysporum* f. sp. *lactucae*, the cause of Fusarium wilt of lettuce. Until recently, three races (1, 2 and 3) of the pathogen had been identified by their ability to cause disease on differential lettuce cultivars, and using molecular tools. Race 4 was identified in the Netherlands and in Italy (Gilardi *et al.*, 2019). Pathogenicity tests in controlled environmental conditions showed that none of the commercial lettuce cultivars popular in Italy are completely resistant to race 1 of *F. oxysporum* f. sp. *lactucae*, and only 57% of the tested cultivars were resistant to race 2, and 21% were resistant to race 3.

Almost all currently available commercial hybrids of muskmelon (*Cucumis melo*) possess FOM-1 and FOM-2 genes, conferring resistance to the physiological races 0, 1 and 2 of *F. oxysporum* f. sp. *melonis*. However, none of these hybrid hosts are resistant to the race 1-2 of this pathogen, which has occurred in all major production areas in Italy since the 1990s. No commercial hybrids of pepper are completely resistant to *P. capsici* due to the variability of this pathogen, which in Italy is also a major pathogen of tomato and cucumber grown in plastic greenhouses. *Fusarium oxysporum*, because of genetic variability and ability to evolve, encompasses *formae speciales* infecting aromatic flower plants (Gullino *et al.* 2012; Gullino *et al.*, 2015). New *formae speciales* of this pathogen have been frequently reported in nurseries of ornamentals in Italy (Garibaldi *et al.*, 2012; Matic *et al.*, 2018; Ortu *et al.* 2018).

HOST SHIFTS AND EXPANSION OF HOST RANGES

Polyphagous soil-borne plant pathogens, including *S. sclerotiorum*, *S. rolfsii*, *P. cinnamomi*, *P. nicotianae*, *P. palmivora* and *P. niederhauserii*, infecting very many host plant species, usually widen their host ranges when they invade new areas rich in biodiversity. These areas include natural ecosystems, nurseries of ornamentals, and complex agricultural systems, so the pathogens come into contact with potential new host plants. General pathogens are better invaders than specialists, due to their non-selective ability to seek new hosts in a new environment (Navaud *et al.*, 2018; Thines 2019). Although specialized pathogens may infect new hosts less frequently, the host range expansion of *formae speciales* of *F. oxysporum* to include plant species of the same family is quite common. A new *forma specialis* (f. sp.) of *F. oxysporum*, *F. oxysporum* f. sp. *papaveris*, was discovered in the Liguria region (northern Italy) on Iceland poppy (*Papaver nudicaule*) a plant native to Arctic regions of North America and Eurasia (Garibaldi *et al.* 2012; Ortu *et al.* 2015). The pathogen was initially thought to have been introduced through contaminated seeds (Bertetti *et al.* 2015). However, the high susceptibility of artificially inoculated *Chelidonium majus* and *P. rhoeas*, two species of *Papaveraceae* endemic in Italy, to *F. oxysporum* f. sp. *papaveris*, supports the hypothesis that this f. sp. was already present in Liguria, and shifted onto Iceland poppy from wild relatives (Bertetti *et al.*, 2018a).

The report of *F. oxysporum* f. sp. *chrysanthemi* on orange coneflower (*Rudbeckia fulgida*) in Northern Italy, has expanded the list of hosts of this f. sp., including several other ornamental plants of the *Asteraceae* such as chrysanthemum, Paris daisy, African daisy, and gerbera (Matic *et al.* 2018).

INTRODUCTION, OR GEOGRAPHIC RANGE EXPANSION OF SUSCEPTIBLE HOST PLANTS

When an exotic plant is introduced into a new geographical area, there is justified concern about the risk of it being a vehicle for alien pathogens (Eschen *et al.* 2019), while its susceptibility to pathogens already established in the area is often overlooked. It is more likely for new hosts to be susceptible to native pathogens if components of the resident flora are closely related to the introduced host or if polyphagous pathogens are present in the area. One example is avocado (*P. americana*), whose culture is rapidly expanding in southern Italy. This tropical fruit tree is susceptible to white root

rot caused by *Rosellinia necatrix*, which is a well-known and widespread pathogen of olive and fruit trees in Italy (Skena *et al.*, 2008; Pasini *et al.*, 2016). White root rot is regarded as a major disease of avocado in Spain, the most important avocado producing country in the Mediterranean Basin. Selection for tolerant rootstocks was carried out, but this was probably not completely successful because integrated management strategies are being sought (Ruano-Rosa *et al.*, 2018a). The disease is a serious threat to the avocado industry in Italy, that currently relies on *P. cinnamomi*-tolerant rootstocks for sustainable production. Molecular diagnostic methods to detect the pathogen in soil and host tissues are available (Skena *et al.*, 2002; Skena *et al.*, 2013), and these could be useful tools to prevent introduction with infected nursery plants or to select non-infested planting sites.

Verticillium wilt caused by *V. dahliae* and Phytophthora crown and root rot caused by *Phytophthora* spp. are common diseases in several traditional crops in Italy, and these pathogens have been recently reported on goji (*Lycium barbarum* L.). This plant, producing edible fruit, is native to China, and was introduced into Italy and grown commercially from only a few years ago. Although goji can is a minor crop, it has become very popular due to the vaunted health benefits of its berries. Verticillium wilt of young plants of goji has been reported in Calabria (Ruano-Rosa *et al.* 2017), while crown and root rot caused by *P. nicotianae* have been reported in Apulia (Cariddi *et al.* 2018).

AVAILABILITY OF FUNGICIDES AND DEVELOPMENT OF FUNGICIDE RESISTANCE

Limited availability of fungicides and the development of fungicide resistance can be relevant as factors fostering emergence of soil-borne diseases in nurseries and agricultural systems. Insensitivity to metalaxyl among isolates of *P. capsici* causing Phytophthora blight of pepper has been reported in southern Italy since the 1990s (Pennisi *et al.*, 1998). In a European-wide sample of 77 *P. ramorum* isolates collected in 2004, 24% were resistant to mefenoxam (Brasier, 2008). Phenylamide fungicides, including compounds such as metalaxyl, metalaxyl-M (mefenoxam) and benalaxyl, are frequently used against damping-off caused by *Pythium*. Resistance to phenylamides appeared shortly after their commercialization, in populations of various plant pathogenic oomycetes, including several *Pythium* spp. such as *P. aphanidermatum*, *P. dissotocum*, *P. heterothallicum*, *P. irregulare*, *P. cylindrosporium*, *P. splendens*, *P. torulosum* and *P. ultimum* (Moorman *et al.*, 2002; Taylor *et al.*, 2002).

A recent study by Matic *et al.* (2019), with 53 isolates of six *Pythium* species (*P. ultimum*, *P. aphanidermatum*, *P. irregulare* complex, *P. sylvaticum*, and *Pythium* ClusterB2a sp.) obtained from different vegetable hosts, showed that they were all sensitive to azoxystrobin, with small variations in their species-specific baseline sensitivity. As a consequence, this fungicide may be effectively applied regardless of the pathogen or host species involved. Conversely, precise *Pythium* species identification and sensitivity tests of isolates may be crucial for reliable use of mefenoxam, as baseline sensitivity to this fungicide varies greatly among species, and resistant isolates may occur in field populations of a sensitive species (Matic *et al.*, 2019).

A relevant example of the emergence of diseases due to restrictions in the use of fungicides is the emergence or re-emergence of endemic soil-borne pathogens of vegetable crops after the phasing out of methyl bromide. Without soil fumigation, soil-borne pathogens considered minor, such as *C. coccodes* on tomato and pepper, have emerged, and well-known major pathogens, such as *P. capsici* on pepper and tomato, *S. sclerotiorum*, *R. solani*, *F. oxysporum* f. sp. *lactucae* and *Verticillium dahliae* on lettuce, and *S. sclerotiorum* and *R. solani* on *Solanum* or cucurbit hosts, have re-emerged (Garibaldi *et al.*, 2008; Gilardi *et al.* 2014a,b). The implications of phasing-out of methyl bromide for the management of diseases of vegetable crops in Europe have been addressed by exhaustive reviews (Lazarovits and Subbarao, 2010; Colla *et al.*, 2012).

In the last 10 years, cases of resistance to diverse classes of fungicides have been reported in populations of *Calonectria* and *Phytophthora* species in nurseries of ornamentals in Southern Italy (Vitale *et al.* 2009; Guarnaccia *et al.* 2014; Aiello *et al.* 2018). These cases document the failures to control already established soil-borne polycyclic diseases as results of excessive and improper use of fungicides to control diseases of ornamental plants. The emergence of fungicide resistance in nursery populations of pathogens that have wide host ranges, such as *Phytophthora* and *Calonectria*, is a potential threat for other agricultural systems, because these fungicides are part of integrated pest management (IPM) strategies for many horticultural crops. More ecological approaches, such as the use of pathogen-suppressive soil mixtures or substrates (Hoitink *et al.*, 1997; Hoitink and Boehm, 1999; Raviv, 2008; Pugliese *et al.*, 2012; Cesarano *et al.*, 2017a; Pascual *et al.*, 2018; De Corato *et al.*, 2019), and systems-based methods, can be alternatives to the intensive use of fungicides for the management of polycyclic soil-borne diseases in ornamental plant nurseries. Systems-based approaches are

disease management strategies that have evolved from IPM concepts, and these incorporate agricultural practices fostering disease suppressive soil microbial communities into the cropping system design (Chellemi *et al.*, 2016).

CHANGES OF CROPPING SYSTEMS

Shifts in farming practices and agricultural techniques, such as propagation methods, soil management types, planting densities and irrigation systems, or the substitution of cultivars or rootstocks, may trigger the emergence or re-emergence of soil-borne plant diseases. The disease consequences of the introduction and the large-scale use of grafted plants in intensive and soil-less vegetable crops in Italy, fostered by the phasing-out of methyl-bromide, have changed cropping systems, and this can be a major driving factor of the emergence or resurgence of soil-borne fungal diseases (Gilardi *et al.*, 2013; Gilardi *et al.*, 2014 a, b, c.). Although most rootstocks of *Solanum* or cucurbit crops possess multiple resistances, none tolerate all the potential soil-borne pathogens of a particular crop. Resistance of different rootstocks to a single pathogen also varies greatly, and in some cases resistance may be overcome by high inoculum pressure and environmental conditions conducive for the disease. This has occurred for infections from *V. dahliae* on eggplant grafted on *S. nigrum*, and for *P. nicotianae* on tomato grafted on tomato hybrid rootstocks 'Beaufort' and 'He Man' (*Solanum lycopersicum* x *S. hirsutum*) (Gilardi *et al.*, 2011).

Change and intensification of cultivation systems may favour emergence of soil-borne fungal diseases in traditional tree crops. This is the case with Verticillium wilt (*V. dahliae*) and Phytophthora root rot (*Phytophthora* spp.) in olive orchards, as a consequence of the expansion of intensive and super-intensive planting systems (Cacciola *et al.*, 2011a; Jiménez-Díaz *et al.*, 2012). Mixed infections of both diseases have also been reported in Italy (Lo Giudice *et al.*, 2010). Verticillium wilt is the most serious disease of olive in Spain (López-Escudero and Mercado-Blanco, 2011), the most important world olive-producing country. In Italy, Verticillium wilt is regarded as a major disease of olive in Apulia (Nigro *et al.*, 2005), the most important olive-producing region, and is increasingly becoming a serious problem in new plantings. In Calabria and Sicily this disease occurs sporadically. Verticillium wilt also occurs on old trees, but symptoms are usually less severe and transient, as mature trees may recover spontaneously. Particular attention has been paid to irrigation as a factor favour-

ing the increasing incidence and severity of Verticillium wilt in young, intensive and super-intensive olive plantations (Pérez-Rodríguez *et al.* 2016; Santos-Rufo *et al.*, 2017). However, numerous other factors are involved in the emergence of this disease, including infected planting (rooted-cuttings) and propagation material, establishment of new orchards in infested soils, spread of virulent *V. dahliae* strains of the D (defoliating) pathotype, and susceptibility of many popular cultivars, such as 'Arbequina' and 'Arbosana', which are widely used in super-intensive plantings. These and additional factors contributing to the emergence of Verticillium wilt in olive orchards are discussed in detail in the review on this disease by López-Escudero and Mercado-Blanco (2011). In Italy, evaluation of susceptibility of olive cultivars to the disease, and the search for resistant rootstocks, have potential for management of this disease (Bubici and Cirulli, 2012).

Pomegranate (*Punica granatum*) is another traditional fruit tree, native to the region extending from modern-day Iran to northern India. This plant has been cultivated since ancient times throughout the Middle East, Caucasus and Mediterranean region for its edible fruit. Recent intensive cultivation of this deciduous shrub, and establishment of modern commercial orchards for increasing yields, are posing new disease problems that could be serious constraint to expansion of this fruit crop in southern Italy. Crown and root rots caused by *Coniella* (syn. *Pilidiella*) *granati* are emerging soil-borne diseases in irrigated pomegranate orchards. This pathogen has been recently reported in Apulia, Basilicata, and Calabria regions (Pollastro *et al.*, 2016), and occurs in many other pomegranate-producing countries, including China, Iran, Spain, Greece and Turkey. *Coniella granati* may also cause pomegranate fruit rots. No effective management strategy is available for crown and root rot caused by this pathogen.

MONOCULTURE

It is commonly assumed that continuous cultivation of one crop, or crops of the same family, in the same soil results in increased inoculum of soil-borne pathogens, and increased incidence of root diseases, with consequent detrimental effects on crop yields. There is extensive evidence that reduction of biodiversity due to monoculture leads to development of detrimental soil conditions, that limit the cultivation of the same crop. This phenomenon, known in agriculture since ancient times but not fully explained, has been called "soil sickness". More recently, plant ecologists have preferred the more

comprehensive term negative plant-soil feedback (NPSF). This concept stresses the negative feedback between plant and soil, and includes agro-ecosystems and natural plant communities (Cesarano *et al.*, 2017b). Soil sickness is a serious concern for staple, cash, vegetable, forage, flower, ornamental and fruit tree crops (Bonanomi *et al.*, 2007; Bonanomi *et al.*, 2011a,b), including major crops such as wheat, maize, rice, sugarcane, alfalfa, soybean, grape, peach, apple, olive, citrus, tea and coffee. Three fundamental hypotheses have been put forward to explain soil sickness. These are: i) soil nutrient depletion or imbalance; ii) release of autotoxic compounds as root exudates or during decomposition of crop residues; and iii) build up of inoculum of soil-borne pathogens and corresponding modification in soil microbiomes, i.e. shifts in the soil microbial community structure from beneficial, including mycorrhizae, to detrimental microorganisms (Cesarano *et al.*, 2017b). The effectiveness of soil sterilization or soil treatments with fungicides in restoring crop productivity has been regarded as the most convincing proof supporting the hypothesis that plant pathogens are major determinants of soil sickness (Cesarano *et al.*, 2017b). In Italy, the build-up of inoculum of several soil-borne fungal pathogens has been implicated in apple replanting problems and in the black root rot complex of strawberry (Manici *et al.*, 2003; 2005). Soil sickness due to *Phytophthora* spp. is causing the decline of lentil (*Lens culinaris*) crops on the island of Ustica (Puglisi *et al.*, 2016), a small island in the Tyrrhenian sea 38 km north of Sicily. The local landrace of lentil, appreciated by consumers and recently recognized as a Slow Food Presidium, is grown as a monocrop.

CONCLUSIONS

Based on published reports, most of the recently emerging diseases in Italy have been caused by pathogens introduced from other countries. Although emerging disease occurrence is partly distorted by the greater attention paid to discoveries of exotic pathogens and the rapidity with which the news of the emergence of new pathogens is delivered, this can mainly be imputed to the failure of the current phytosanitary system to prevent the introduction of alien pathogens, and confirms the need to reinforce this system. The EU regulation 2016/2031, which becomes fully effective in December 2019, demonstrates that there is awareness of the problem, and has addressed biosecurity by introducing major changes in phytosanitary regulations. This regulation aims to prevent introduction, establishment, and spread of harmful organisms for plants, and to coordinate and

harmonize efforts made by different countries throughout the European Union. Similarly, an efficient phytosanitary certification system for propagation materials and nursery plants is the only effective means to prevent the spread of introduced and native pathogens within individual countries. These systems may be mandatory or voluntary, and must include forestry and landscape nursery plants as there is considerable evidence that these plants may be “Trojan horses” for the introduction and spread of invasive soil-borne plant pathogens in natural and forestry ecosystems. These ecosystems are particularly vulnerable, as eradication or mitigation of the effects of harmful pathogens in these ecosystems are not feasible or is more problematic than in agricultural systems.

Another way to reduce the risk of introduction and spread of exotic pathogens is to develop modern and self-sufficient national nursery production systems. In this regard Italy, which was able to meet domestic demand for nursery plants in strategic sectors, such as citrus, olive, fruit and nut trees crops, increasingly relies on imports from other countries. Plant material for ornamental, forestry, and staple and horticultural crops such as potato and strawberry, is also imported into Italy.

Application of phytosanitary regulations and the success of phytosanitary certification systems depend largely on the availability of adequate diagnostic methods, which have to be continuously updated to accommodate the rapid evolution of nomenclature and molecular taxonomy of fungi (Rossman and Palm-Hernandez, 2008; Groenewald *et al.*, 2011; Stielow *et al.*, 2015). These systems must be specific, sensitive, rapid, reproducible and practical. In the last 20 years, a large number of molecular methods for the detection of soil-borne fungal plant pathogens have been published in the scientific literature (Schena *et al.*, 2013). However, very few of these methods have been validated or applied routinely on large-scales, while some lack specificity which is a basic requirement (Blomquist *et al.*, 2005; Kunadiya *et al.*, 2017). Development of new and more specific molecular diagnostic methods is facilitated by the availability of whole genomes for a growing number of fungi and oomycetes (Feau *et al.*, 2019). Innovative and promising approaches for diagnoses of soil-borne pathogens include multiplex assays for genus- and species-specific detection of *Phytophthora* in environmental samples (Scibetta *et al.*, 2012; Bilodeau *et al.*, 2014), mRNA-based protocols to circumvent the problem of false positives due to the detection of DNA of non-viable propagules (Chimento *et al.*, 2012; Kunadiya *et al.*, 2019), isothermal amplification assays for *in situ* detection of *Phytophthora* spp. in plant tissues (Miles *et al.*, 2014), and PCR-based meth-

ods for the identification of *formae speciales* and races of *F. oxysporum* from seeds, plants and soil samples (Pasquali *et al.*, 2008; Mbofung and Pryor, 2010; Srinivasan *et al.*, 2010; Lievens *et al.*, 2012; Gilardi *et al.*, 2017; Thomas *et al.*, 2017). Recently, a loop-mediated-isothermal amplification (LAMP) assay using a panel of target and non-target species was developed for detection of *Fusarium oxysporum* f. sp. *lactucae* in soil, lettuce seeds and plants. This assay is a significant advantage over the traditional methods, which do not allow clear discrimination of the *formae speciales* of *F. oxysporum* (Franco Ortega *et al.*, 2018). The taxonomy of *F. oxysporum* is evolving, so this will affect evaluation and interpretation of results obtained with these new diagnostic methods. Very recently, this taxonomy has been substantially modified and several cryptic species (so far 15) have been resolved within this species complex (Lombard *et al.*, 2019).

Next-generation sequencing approaches, which identify microorganisms in terms of operational taxonomic units, remain too expensive to be used as routine diagnostic methods, and the results are not precise enough to be used for quarantine or certification purposes. Conversely, as shown for aerial plant pathogens (Mosca *et al.*, 2014; Abdelfattah *et al.*, 2016), high-throughput sequencing could be an appropriate tool for studying the complexity and ecological functions of soil microbiota, its role in soil suppressiveness and negative plant-soil feedback, its interactions with soil-inhabitant pathogens, and effects of soil management practices on microbial population dynamics and functionality (Bonanomi *et al.*, 2016; Gómez Expósito *et al.*, 2017; Schlatter *et al.*, 2017; Ampt *et al.*, 2018).

Climate change, whose most evident effect is the rise in temperatures, has often been presumed to be responsible for the emergence of soil-borne diseases, simply because they were caused by thermophilic or mesophilic pathogens. This over simplification causes direct and indirect effects of climate change to be underestimated, and disease emergence drivers, such as severe weather events or conducive environmental conditions, which here have been considered distinct, may themselves be a consequence of climate change. Natural ecosystems are generally more vulnerable to the effects of climate changes, while in agricultural systems these effects can be mitigated by active interventions, such as irrigation during dry periods or the use of genotypes resistant to biotic or abiotic stress factors. Conversely, other disease emergence drivers, such as the genetic mutation of pathogens, prevail in agricultural systems due to the selective pressure exerted by the genetic uniformity of the host on the pathogen. In general, host genetic uni-

formity and susceptibility have crucial roles in determining invasion success and spread dynamics of plant pathogens after introduction and establishment, so monocultures of genetically similar or identical plants are severely impacted by invasive pathogens. It is generally assumed that biodiversity of natural ecosystems give them resilience against invasive exotic pathogens, but if the invader is a polyphagous pathogen, such as *P. cinnamomi* or *P. ramorum*, the result is a loss of biodiversity. It is, therefore, not easy to predict and evaluate the impacts of emerging diseases, as the emergence driving factors are numerous and complex, often interacting with each other.

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