

Current Status of *Fusarium oxysporum* *Formae Speciales* and Races

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ABSTRACT

The *Fusarium oxysporum* species complex includes both plant pathogenic and nonpathogenic strains, which are commonly found in soils. *F. oxysporum* has received considerable attention from plant pathologists for more than a century owing to its broad host range and the economic losses it causes. The narrow host specificity of pathogenic strains has led to the concept of *formae speciales*, each *forma specialis* grouping strains with the same host range. Initially restricted to one plant species, this host range was later found to be broader for many *formae speciales*. In addition, races were identified in some *formae speciales*, generally with cultivar-level specialization. In 1981, Armstrong and Armstrong listed 79 *F. oxysporum formae speciales* and mentioned races in 16 of them. Since then, the known host range of *F. oxysporum* has considerably increased, and many new *formae speciales* and races have been identified. We carried out a comprehensive search of the literature to propose this review of *F. oxysporum formae speciales* and races. We recorded 106 well-characterized *formae speciales*, together with 37 insufficiently documented ones, and updated knowledge on races and host ranges. We also recorded 58 plant species/genera susceptible to *F. oxysporum* but for which a *forma specialis* has not been characterized yet. This review raises issues regarding the nomenclature and the description of *F. oxysporum formae speciales* and races.

Keywords: diversity, *forma specialis*, host specificity, host range, pathogenicity, race, root rot, vascular wilt.

The *Fusarium oxysporum* Schlechtend. species complex is comprised of soilborne fungi found in cultivated and uncultivated soils worldwide under various climates (Burgess 1981; Joffe and Palti 1977; Kommedahl et al. 1988; Mandeel et al. 1995). This species complex includes plant pathogens, human pathogens, and many nonpathogens. Pathogenic strains are morphologically indistinguishable from nonpathogenic strains. *F. oxysporum* displays high functional and genetic diversity (Kistler 1997; Nelson et al. 1981; O'Donnell et al. 2009; Steinberg et al. 2016). Evidence of its diversity lies in its impressive plant host range, which includes both dicots (e.g., bean, carnation, and tomato) and monocots (e.g., banana, orchids, and palms). Pathogenic *F. oxysporum* can affect perennial and annual plants, including mostly land-based, but also aquatic plants (e.g., lotus). From a practical point of view, pathogenic *F. oxysporum* strains cause wilts or root and crown rots on economically important field crops (banana, cotton, soybean),

many market garden crops (melon, onion, and tomato), as well as ornamental crops (cyclamen, gerbera, and orchids), and even on weeds or parasitic plants (broomrape and witchweed). However, individual strains display selective pathogenicity to a more or less narrow range of host plants. Strains with the same host range, generally one plant species, are grouped into a *forma specialis*. For example, strains responsible for *Fusarium* wilt of tomato belong to the *forma specialis lycopersici*, while those causing wilting on banana belong to the *forma specialis cubense*. The *forma specialis* concept was first created to distinguish strains of *Puccinia graminis* Pers. displaying similar morphological features but different host ranges. This new rank was designated as “spezialisierten formen” (Eriksson 1894). A definition was given in 1910 during the International Botanical Congress of Brussels: “In the case of parasites, especially parasitic fungi, authors who do not give specific value to forms characterized from a biological standpoint but scarcely or not at all from a morphological standpoint, should distinguish within the species special forms (*forma specialis*, f. sp.) characterized by their adaptation to different hosts” (Proceedings of the 3rd International Botanical Congress, 1910, Brussels Chapter II, Recommendation I bis). Since 1930, the existence of this intraspecific rank has been admitted by the International Code of Botanical Nomenclature (commonly named International Code of Nomenclature for algae, fungi and plants), but it is not codified by this international authority because accepting physiological traits represents a hurdle (Gordon 1965). Snyder and Hansen (1940)

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reported 25 “biologic forms” within *F. oxysporum* based on their host ranges. In 1965, *F. oxysporum* pathogenic strains were no longer designated as forms but as *formae speciales* (f. sp.) (Gordon 1965). In addition, some *formae speciales* are subdivided into races, defined by cultivar-level specialization and, in some cases, by known resistance genes in these cultivars (Gordon and Martyn 1997). Much attention has been devoted to *F. oxysporum* over the last hundred years; it is still among the most important fungal plant pathogens based on its scientific and economic importance (Dean et al. 2012). New *formae speciales* and races are regularly described, but their list has not been updated for more than 35 years (Armstrong and Armstrong 1981). We searched the scientific literature and extension journals to propose this review of currently described *F. oxysporum formae speciales* and races, and of the plant species susceptible to *F. oxysporum* diseases. This review also raises issues regarding the nomenclature and the description of *F. oxysporum formae speciales* and races.

DISEASES CAUSED BY *F. OXYSPORUM*

Knowledge on root infection by *F. oxysporum* was recently reviewed (Gordon 2017). Pathogenic *F. oxysporum* strains are responsible for two types of symptoms, i.e., most often vascular wilting and in some cases rotting. *F. oxysporum* causing vascular wilting penetrates the host roots to reach the xylem vessels, which it colonizes upwards, resulting in progressive yellowing and wilting of the plant (Olivain and Alabouvette 1999). This type of symptom is the most commonly encountered one. According to the Committee on standardization of common names for plant diseases, it is associated with several disease names that are Fusarium yellows, Fusarium blight, and Fusarium wilt (The American Phytopathological Society on the standardization of common names for plant diseases, 2017; <http://www.apsnet.org/publications/commonnames/Pages/default.aspx>). *F. oxysporum* that causes rotting progresses in the roots and hypocotyl cortical tissues without reaching the vascular system (Jarvis and Shoemaker 1978). Its growth causes the formation of discolored tissues evolving into brown to black necrotic spots that end up in the rotting of the plant. Diseases with rotting symptoms are called basal rot, Fusarium stem rot, or crown and root rot. Rot diseases predominantly affect plants with storage organs such as bulbs (e.g., lily), corms (e.g., crocus), tubers (e.g., potato), and rhizomes (e.g., ginger) (Boerema and Hamers 1988, 1989; Manici and Cerato 1994; Trujillo 1963). As such organs are characterized by a shortened stem, we may hypothesize that the fungus adjusts its progression strategy in the plant tissues according to the anatomical peculiarity of the plant. The first case of rot disease caused by *F. oxysporum* was reported on lupine (Weimer 1944). To distinguish root-rot-producing strains from those producing typical vascular wilt, Weimer (1944) proposed the name *F. oxysporum* f. sp. *radicis-lupini*. Since then, the term “*radicis*” has differentiated rot-producing strains from wilt-producing strains. The *formae speciales* causing rot were taken into account in Gordon’s review (Gordon 1965) but were removed from subsequent reviews (Armstrong and Armstrong 1968, 1981). However, the scientific community accepted the concept of “*radicis*”-type *forma specialis*. For example, *formae speciales radicis-lycopersici* and *radicis-cucumerinum* are recognized as such for the root rot they cause on tomato and cucumber, respectively (Jarvis and Shoemaker 1978; Vakalounakis 1996). Including the term “*radicis*” in the name of the *forma specialis* allows for an immediate identification of the type of symptoms. However, some *formae speciales*, for example *cepae*, *lilii*, and *opuntarium*, cause rotting but are not referred to as *formae speciales* “*radicis*-host plant name” (Baayen et al. 1998; Brayford 1996; Polizzi and Vitale 2004). On the other hand, *F. oxysporum* that causes disease on vanilla was initially described as *forma specialis vanillae*, but it was recently renamed *forma specialis radicis-vanillae* regarding the disease symptoms it causes (Koyyappurath et al. 2015). Nevertheless, some plants can be attacked by two different *formae*

speciales causing the two types of symptoms. For example, tomato is susceptible to the *formae speciales lycopersici* causing wilt and *radicis-lycopersici* causing rot. In rare cases, damping off caused by *F. oxysporum* has also been reported, on Pinaceae and on *Allium cepa* for instance (Abawi and Lorbeer 1972; Bloomberg 1971; Stewart et al. 2012). Pathogenic *F. oxysporum* strains are occasionally reported as part of a consortium of pathogens (Beccari et al. 2010).

HOW MANY *F. OXYSPORUM FORMAE SPECIALES* AND RACES?

The latest review that many scientists still refer to dates back to more than 35 years (Armstrong and Armstrong 1981). The authors reported 79 *formae speciales* and mentioned races in 16 *formae speciales*. Since then, the known host range of *F. oxysporum* has considerably increased, and many new *formae speciales* and races have been described. Through a comprehensive review of the literature (up to August 2018), we counted 106 *formae speciales* that we considered to be well documented (Table 1), 37 *formae speciales* that we considered as insufficiently documented (Table 2), and 58 additional host plants for which no *forma specialis* has been characterized so far (Table 3).

The host range of the *formae speciales* listed in Table 1 consists of plants belonging to 45 families, among which Asteraceae, Cucurbitaceae, Fabaceae, and Solanaceae are the most represented. Symptoms caused by these *formae speciales* correspond mainly to wilt, and for some of them to rot. Some *formae speciales* were described very recently, such as the *formae speciales lavandulae*, *cichorii*, *crassulae*, and *mori* (Ortu et al. 2013, 2018; Pastrana et al. 2017; Poli et al. 2012). The initially restricted host range was expanded from one to several plant species for many *formae speciales* (see next section). Races mostly based on cultivar-level specialization were identified in 25 of the 106 *formae speciales* listed in Table 1. However, the notion of race is not always used in the same way by authors, and this makes it difficult to characterize pathogenic variants within *F. oxysporum*. For example, pathogens of different Brassicaceae species have been described as different *formae speciales* (*conglutinans*, *matthioli*, and *raphani*), or as races of the *forma specialis conglutinans* (Table 1). Therefore, special focus is brought to the concept of race in a following section.

Table 2 groups 37 *formae speciales* that we consider as insufficiently documented. These *formae speciales* mainly correspond to (i) pathogens isolated from diseased plants and assigned to a *forma specialis* without having been inoculated on the plant species of origin to confirm their pathogenicity, (ii) pathogens whose host specificity was not analyzed, and (iii) pathogens reported in Gordon’s (1965) or Armstrong and Armstrong’s (1968, 1981) reviews for which we did not have access to a publication describing the *forma specialis*. Moreover, some pathogens initially identified as *F. oxysporum* may belong to other closely related species such as some strains causing disease on pine and which actually belong to the recently described species *F. commune* (Gordon et al. 2015). We also included in Table 2 the *formae speciales cucurbitacearum* and *iridacearum* that have been proposed to group all *formae speciales* pathogenic on plants from the families Cucurbitaceae and Iridaceae, respectively (Gerlagh and Blok 1988; Palmero et al. 2014; Roebroek 2000).

Furthermore, the host range of *F. oxysporum* is regularly extended with the emergence of new diseases. We recorded 58 plant species or genera in the literature described as susceptible to *F. oxysporum* but whose *forma specialis* has not been characterized yet (Table 3). These 58 host plants belong to 38 different families, among which 17 are not identified in Tables 1 and 2. A total of 45 of these 58 new host plants were reported very recently, i.e., in the 2000s. The diseases caused by these “new” pathogens are mostly wilt, rot to a lesser extent, and more rarely a few other symptoms (Table 3). It is likely that the number of *F. oxysporum formae*

speciales and races will keep increasing in the future. *F. oxysporum* host plants have been identified on all continents except the Antarctic, and its overall host range listed in the three tables presented in this review includes 73 different plant families that already represent a large host spectrum. In addition, most of these known hosts are plants of agronomic and ornamental interest, which for practical and economic reasons have so far attracted more attention than wild plants. The current need to control weeds by alternatives to chemical methods reveals that these plants are also infested by pathogens, including *F. oxysporum* strains that are potential candidates for weed biological control (Boari and Vurro 2004; Elzein et al. 2008). Moreover, the distribution of *F. oxysporum* is ubiquitous, so that there is a good chance that new *F. oxysporum*-host plant interactions, and thus new *formae speciales* will soon be revealed in addition to those already proposed (Table 3). Such a wide geographical distribution and wide host spectrum confirms the adaptability of *F. oxysporum* to the diverse biotic and abiotic environmental conditions encountered worldwide (Steinberg et al. 2016).

AN EVOLVING *FORMA SPECIALIS* CONCEPT?

F. oxysporum formae speciales are mainly described as highly specific. Their host range was initially supposed to be restricted to one plant species, but it was found to be broader for many *formae speciales* over time. Only 53 of the 106 *formae speciales* listed in Table 1 remain associated with a unique plant species to date. This number can even be less, based as few potential hosts have been tested even for well-studied *formae speciales*. Thus, the actual host range for any given *forma specialis* could well be much wider than currently recognized. Several of them were found to be pathogenic to (i) several species within a genus, e.g., *forma specialis narcissi*, or (ii) several genera within a plant family, e.g., *forma specialis gladioli* that is pathogenic to different Iridaceae plants, or finally (iii) plants belonging to different families, e.g., *forma specialis vasinfectum* (Table 1). Some plant species may be more permissive than others to various fungal attacks. Thus, Maltese cross appears to be a secondary host for three different *formae speciales* (*conglutinans*, *dianthi*, and *spinaciae*) (Table 1). The difficulty in defining the host specificity of *F. oxysporum* pathogenic strains is confounding for several *formae speciales*. That is why cross-pathogenicity of *formae speciales cucumerinum*, *niveum*, *lagenariae*, and *luffae* on their respective host plants led Gerlagh and Blok (1988) to propose to group all *formae speciales* pathogenic on cucurbitaceous crops into the new *forma specialis cucurbitacearum*. The situation is also confused for *F. oxysporum* that attacks iridaceous crops. *Formae speciales gladioli*, *croci*, and *saffrani* have all been described as pathogenic on *Crocus* spp., and the host range of the *forma specialis gladioli* includes several Iridaceae genera. Roebroek (2000) proposed to assign all the strains pathogenic to iridaceous crops to a new *forma specialis* called *iridacearum*.

Half of the *formae speciales* described so far (Table 1) are, to our current knowledge, each pathogenic to one host plant only, while the other half includes strains whose interaction specificity is much wider and sometimes leads to cross-pathogenicity. It is always possible to think that the conditions under which pathogenicity tests are carried out favor the infection of plants by strains that may not necessarily be pathogenic in natural situations. However, it is difficult to imagine that half of the tests performed so far were “false positives” caused by too high inoculum doses. Nevertheless, most of the extended host ranges reported in Table 1 were obtained under artificial inoculation conditions. This was not the case for the *forma specialis radiscucumerinum* that attacked cucumber but also melon under natural conditions (Vakalounakis et al. 2005).

It is now well documented that a strain of *F. oxysporum* pathogenic to a given host plant can be genetically closer to a strain

pathogenic to another plant species, or even closer to a non-pathogenic strain than to a strain pathogenic to the same host plant (Baayen et al. 2000; Fourie et al. 2009; Inami et al. 2014; O'Donnell et al. 2009). The existence of many transposons is likely to generate mutations leading to the expression of different effectors (Chalvet et al. 2003; Daboussi and Capy 2003). Horizontal gene transfer is another mechanism that can explain genetic diversity among strains that are pathogenic to a given plant species (Ma 2014). Horizontal gene transfer may also explain cross-pathogenicity phenomena. Horizontal gene transfer between pathogenic and nonpathogenic *F. oxysporum* strains has indeed been demonstrated under controlled conditions, but competition among *F. oxysporum* populations at the plant root surface in the host plant rhizosphere provides favorable conditions for such horizontal gene transfers.

SPECIAL FOCUS ON THE CONCEPT OF RACE

The concept of physiological race was mentioned for *Puccinia graminis* in 1913 (Stakman 1913). It was defined as “a biotype or group of biotypes, within a species or lower taxon, which can be distinguished with reasonable facility and certainty from other biotypes or groups of biotypes by physiologic characters, including pathogenicity” (Stakman et al. 1962). Like the *forma specialis*, the race is not a formal taxonomic rank and is not codified by the International Code of Nomenclature for algae, fungi and plants. Therefore, there is no standardized procedure for naming races. They are generally numbered in chronological order of discovery. In some cases, they are defined according to the avirulence genes born by the strains included in the races, or according to the host plant resistance genes they overcome, as in the case of *F. oxysporum* f. sp. *lycopersici* (Alexander and Tucker 1945; Bohn and Tucker 1939). In the absence of a known gene-for-gene relationship, races are often defined according to differential pathogenicity on different cultivars (Habgood 1970). The use of variable criteria to describe new races has led to confusion in several *formae speciales*. For example, up to 11 races were initially described in the *forma specialis pisi* before a revision cut that number down to four (Table 1). In some *formae speciales*, races are described according to climatic predisposition (e.g., *forma specialis cubense* races subtropical and tropical 4), or according to differences in plant symptoms (e.g., *forma specialis melonis* races 1-2 W and 1-2 Y causing wilting and yellowing symptoms, respectively) (Ploetz 2006; Risser et al. 1976). Such subgroupings are convenient as, in some cases, different patterns of symptom development are indicative of genetically distinct strains. *F. oxysporum* races reflect variations in virulence within the *forma specialis*, revealed by differential interactions with different host genotypes sometimes linked to known resistance genes. Thus, the definition of a new race intrinsically requires evaluating the pathogenicity of the strains on several host plant genotypes. The distinction between a *forma specialis* and a race may be narrow in some cases. For example, *forma specialis conglutinans* was initially described as responsible for wilting on Brassicaceae (Kendrick 1930; Pound and Fowler 1951). Later, *forma specialis conglutinans* strains responsible for wilting on stock and radish were reclassified as *forma specialis matthioli* and *forma specialis raphani*, respectively (Baker 1948; Kendrick and Snyder 1942), and later again as races 2 and 3 of *forma specialis conglutinans* (Armstrong and Armstrong 1952, 1981). Later on, Bosland and Williams (1987) restored the *formae speciales conglutinans*, *matthioli*, and *raphani* on the basis of pathogenic and genetic diversity. To avoid such classification issues, races should be ideally based on a gene-for-gene relationship between a pathogenic strain and its host plant; if not applicable, they should be at least defined by a clear-cut cultivar-level specialization.

TABLE 1
***Fusarium oxysporum* formae speciales and races and their corresponding host plants**

<i>Forma specialis</i>	Races	Host plants (common name) ^a	Host plant family	Original references for the description of diseases, <i>formae speciales</i> , races, and host plants ^b
<i>adzukicola</i>	1 to 3	<i>Vigna angularis</i> (adzuki bean)	Fabaceae	Hanzawa 1906; Kitazawa and Yanagita 1984; Kondo and Kodama 1989
<i>aechmeae</i> (syn. <i>aechmea</i>)	None	<i>Aechmea</i> spp.	Bromeliaceae	Gordon 1965; Sauthoff and Gerlach 1957
<i>albedinis</i>	None	<i>Phoenix dactylifera</i> (date palm)	Arecaceae	Killian and Maire 1930; Gordon 1965
<i>allii</i>	None	<i>Allium chinense</i> syn. <i>A. bakeri</i> (rakkyo, Baker's garlic)	Amaryllidaceae	Watanabe and Wakaida 1955; Matuo et al. 1979, 1986
<i>anethi</i>	None	<i>Anethum graveolens</i> (dill)	Apiaceae	Janson 1951; Gordon 1965
<i>angsanae</i>	None	<i>Pterocarpus indicus</i> (angsana)	Fabaceae	Crowhurst et al. 1995; Ploetz 2006b
<i>anoectochili</i>	None	<i>Anoectochilus</i> sp. (jeweled orchid)	Orchidaceae	Huang et al. 2014
<i>apii</i>	1 to 4	<i>Apium graveolens</i> (celery)	Apiaceae	Nelson et al. 1937; Snyder and Hansen 1940; Schneider and Norelli 1981; Puhalla 1984; Epstein et al. 2017
		<i>Pisum sativum</i> (pea)	Fabaceae	Armstrong and Armstrong 1957
		<i>Tithonia rotundifolia</i> (Mexican sunflower)	Asteraceae	Armstrong and Armstrong 1966a
		<i>Asparagus officinalis</i> (asparagus), <i>Gossypium</i> spp. (cotton), <i>Solanum melongena</i> (eggplant)	Asparagaceae, Malvaceae, Solanaceae	Armstrong and Armstrong 1969
<i>arctii</i>	None	<i>Arctium lappa</i> (greater burdock)	Asteraceae	Matsuda and Ozaki 1971; Matuo et al. 1975
<i>asparagi</i>	None	<i>Asparagus officinalis</i> (asparagus)	Asparagaceae	Cohen and Heald 1941; Cohen 1946
<i>basilici</i> (syn. <i>basilicum</i>)	None	<i>Ocimum basilicum</i> (sweet basil)	Lamiaceae	Vergovskii 1956; Dzidzariya 1968
<i>batatas</i>	Between 2 and 4 races	<i>Ipomoea batatas</i> (sweet potato)	Convolvulaceae	Wollenweber 1914; Snyder and Hansen 1940; Smith and Shaw 1943; Armstrong and Armstrong 1958a, 1968; Clark et al. 1998; Rodriguez-Molina et al. 2013
		<i>Nicotiana tabacum</i> (tobacco)	Solanaceae	
		<i>Gossypium</i> sp. (cotton)	Malvaceae	
<i>benincasae</i>	None	<i>Benincasa hispida</i> (wax gourd)	Cucurbitaceae	Gerlagh and Ester 1985; Gerlagh and Blok 1988
<i>betae</i>	None	<i>Beta vulgaris</i> (sugar beet), <i>Amaranthus retroflexus</i> (redroot pigweed)	Amaranthaceae	Stewart 1931; Snyder and Hansen 1940; MacDonald and Leach 1976; Hanson et al. 2018
		<i>Allium cepa</i> (onion), <i>Phaseolus vulgaris</i> (common bean)	Amaryllidaceae, Fabaceae	Webb et al. 2013
		Syn. <i>spinaciae</i> race 2 <i>Spinacia oleracea</i> (spinach)	Amaranthaceae	Armstrong and Armstrong 1976

(Continued on next page)

^a According to the Integrated Taxonomic Information System (ITIS).

^b Supplementary File S1 provides a complete list of the references listed in this table.

TABLE 1
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<i>Forma specialis</i>	Races	Host plants (common name) ^a	Host plant family	Original references for the description of diseases, <i>formae speciales</i> , races, and host plants ^b
<i>bouvardiae</i>	None	<i>Bouvardia</i> sp.	Rubiaceae	Marziano et al. 1987
<i>callistephi</i>	1, 2, 3 (syn f. sp. <i>rhois</i>), 4	<i>Callistephus chinensis</i> (China aster), <i>Tagetes erecta</i> (African marigold), <i>Rhus typhina</i> (staghorn sumac)	Asteraceae, Anacardiaceae	Beach 1918; Snyder and Hansen 1940; Armstrong and Armstrong 1955b, 1971; Olsen 1965
<i>canariensis</i>	None	<i>Phoenix canariensis</i> (Canary Island date palm)	Arecaceae	Mercier and Louvet 1973; Summerell et al. 2001
<i>cannabis</i>	None	<i>Cannabis sativa</i> (hemp)	Cannabaceae	Noviello and Snyder 1962
<i>capsici</i>	None	<i>Capsicum</i> spp. (pepper)	Solanaceae	Leonian 1919; Rivelli 1989; Black 2003
<i>carthami</i>	1 to 4	<i>Carthamus tinctorius</i> (safflower)	Asteraceae	Klisiewicz and Houston 1962; Gordon 1965; Klisiewicz and Thomas 1970a, b; Klisiewicz 1975
<i>cassiae</i>	None	<i>Senna tora</i> syn. <i>Cassia tora</i>	Fabaceae	Armstrong and Armstrong 1954b, 1966c; Gordon 1965
		Several other plant hosts	Several families	Armstrong and Armstrong 1966c
<i>cattleyae</i>	None	<i>Cattleya</i> sp.	Orchidaceae	Foster 1955
<i>cepae</i>	None	<i>Allium cepae</i> (onion)	Amaryllidaceae	Hanzawa 1914; Snyder and Hansen 1940; Brayford 1996a
		Other <i>Allium</i> spp.	Amaryllidaceae	Entwistle 1990; Brayford 1996a
<i>chrysanthemii</i>	3 races	<i>Chrysanthemum</i> × <i>morifolium</i> (chrysanthemum) <i>Argyranthemum frutescens</i> (Paris daisy), <i>Gerbera jamesonii</i> (gerbera), <i>Osteospermum</i> sp. (African daisy), <i>Rudbeckia fulgida</i> (orange coneflower)	Asteraceae Asteraceae	Armstrong et al. 1970; Huang et al. 1992; Troisi et al. 2013 Minuto et al. 2007; Garibaldi et al. 2017; Matic' et al. 2018
<i>ciceris</i> (syn. <i>ciceri</i>)	0, 1A, 1B/C, 2 to 6	<i>Cicer arietinum</i> (chickpea), <i>Cicer</i> spp.	Fabaceae	Prasad and Padwick 1939; Armstrong and Armstrong 1968; Haware and Nene 1982; Trapero-Casas and Jiménez-Díaz 1985; Jiménez-Díaz et al. 1989; Kaiser et al. 1994
<i>cichorii</i>	None	<i>Cichorium intybus</i> (chicory)	Asteraceae	Garibaldi et al. 2011a; Poli et al. 2012
<i>citri</i>	None	<i>Citrus</i> spp.	Rutaceae	Timmer et al. 1979; Timmer 1982; Hannachi et al. 2014
<i>colocasiae</i>	None	<i>Colocasia esculenta</i> (<i>taro</i>)	Araceae	Nishimura and Kudo 1994

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TABLE 1
(Continued from previous page)

<i>Forma specialis</i>	Races	Host plants (common name) ^a	Host plant family	Original references for the description of diseases, <i>formae speciales</i> , races, and host plants ^b
<i>conglutinans</i>	1, 2 (syn. f. sp. <i>raphani</i>), 3 (syn. f. sp. <i>matthioli</i> race 1), 4 (syn. f. sp. <i>matthioli</i> race 2), 5	<i>Brassica oleracea</i> (cabbage), <i>Raphanus sativus</i> (radish), <i>Matthiola incana</i> (stock)	Brassicaceae	Kendrick 1930; Wollenweber 1913; Snyder and Hansen 1940; Armstrong and Armstrong 1952, 1966b; Ramirez-Villupadua et al. 1985; Bosland and Williams 1987
		<i>Silene chalconica</i> syn. <i>Lychnis chalconica</i> (Maltese cross), <i>Valerianella locusta</i> syn. <i>V. olitoria</i> (lamb's lettuce)	Caryophyllaceae, Valerianaceae	Armstrong and Armstrong 1966b; Gilardi et al. 2008
<i>crassulae</i>	None	<i>Crassula ovata</i> (jade plant)	Crassulaceae	Garibaldi et al. 2011b; Ortu et al. 2013
<i>croci</i>	None	<i>Crocus</i> sp. (crocus)	Iridaceae	Boerema and Hamers 1989; Palmero et al. 2014
<i>cubense</i>	1, 2, subtropical race 4, tropical race 4	<i>Musa</i> spp. (banana)	Musaceae	Smith 1910; Snyder and Hansen 1940; Stover and Waite 1960; Ploetz 2006a
		<i>Asparagus officinalis</i> (asparagus)	Asparagaceae	Armstrong and Armstrong 1969
	3 (syn. f. sp. <i>heliconiae</i>)	<i>Heliconia</i> spp. (heliconia)	Heliconiaceae	Waite 1963; Ploetz and Bentley 2001
<i>cucumerinum</i>	1 to 3	<i>Cucumis sativus</i> (cucumber), <i>C. melo</i> (melon syn. muskmelon), <i>Citrullus lanatus</i> syn. <i>C. vulgaris</i> (watermelon)	Cucurbitaceae	van Koot 1943; Owen 1956; Armstrong et al. 1978; Kim et al. 1993
<i>cumini</i>	None	<i>Cuminum cyminum</i> (cumin)	Apiaceae	Patel et al. 1957
<i>cyclaminis</i>	None	<i>Cyclamen persicum</i> (cyclamen)	Primulaceae	Wollenweber and Reinking 1935; Gerlach 1954
		Other <i>Cyclamen</i> spp. (cyclamen)	Primulaceae	Orlicz-Luthardt 1998
<i>delphinii</i>	None	<i>Delphinium</i> spp. (delphinium)	Ranunculaceae	Martin 1922; Laskaris 1949; Kondo et al. 2013
<i>dianthi</i>	1, 2, 4 to 11 (race 3 was reclassified as <i>F. redolens</i> f. sp. <i>dianthi</i>)	<i>Dianthus caryophyllus</i> (carnation)	Caryophyllaceae	Prillieux and Delacroix 1899; Snyder and Hansen 1940; Garibaldi 1975; Baayen et al. 1997
		Other <i>Dianthus</i> spp., <i>Silene chalconica</i> syn. <i>Lychnis chalconica</i> (Maltese cross)	Caryophyllaceae	Armstrong and Armstrong 1954a
<i>echeveriae</i>	None	<i>Echeveria</i> spp.	Crassulaceae	Farr et al. 1989; Ortu et al. 2015a; Garibaldi et al. 2015a
<i>elaeidis</i>	None	<i>Elaeis guineensis</i> (oil palm)	Arecaceae	Wardlaw 1946; Toovey 1949; Gordon 1965
<i>erythroxyli</i>	None	<i>Erythroxylum coca</i> , <i>E. novogranatense</i> (coca)	Erythroxylaceae	Sands et al. 1997

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TABLE 1
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<i>Forma specialis</i>	Races	Host plants (common name) ^a	Host plant family	Original references for the description of diseases, <i>formae speciales</i> , races, and host plants ^b
<i>eucalypti</i>	None	<i>Eucalyptus gonphocephala</i> , <i>E. rudis</i> (eucalyptus)	Myrtaceae	Arya and Jain 1962
<i>eustomae</i>	None	<i>Eustoma grandiflorum</i> (lisianthus)	Gentianaceae	Raabe 1981; Bertoldo et al. 2015
<i>exaci</i>	None	<i>Exacum affine</i> (Persian violet)	Gentianaceae	Elmer and O'Dowd 2001
<i>fabae</i>	None	<i>Vicia faba</i> (broad bean)	Fabaceae	Yu and Fang 1948
<i>fatshederae</i>	None	<i>xFatshedera lizei</i>	Araliaceae	Triolo and Lorenzini 1983
<i>fragariae</i>	None	<i>Fragaria</i> sp. (strawberry)	Rosaceae	Winks and Williams 1965; Brayford 1996b
<i>garlic</i>	None	<i>Allium sativum</i> (garlic)	Amaryllidaceae	Matuo et al. 1986; Brayford 1996a
<i>gladioli</i>	1 and 2	<i>Gladiolus</i> sp. (gladiolus)	Iridaceae	Massey 1926; Snyder and Hansen 1940; Roebroek and Mes 1992
		<i>Babiana</i> sp., <i>Crocus sativus</i> (saffron), <i>Crocus</i> sp. (crocus), <i>Freesia</i> sp. (freesia), <i>Iris</i> sp. (iris), <i>Ixia</i> sp. (corn lily), <i>Sparaxis</i> sp. (wandflower), <i>Streptanthera cuprea</i> , <i>Tritonia</i> spp., <i>Watsonia</i> sp. (bugle lily)	Iridaceae	McClellan 1945; Di Primo et al. 2002
<i>glycines</i>	None	<i>Glycine max</i> (soybean)	Fabaceae	Armstrong and Armstrong 1965a
<i>hebae</i> (syn. <i>habae</i> , <i>hebe</i>)	None	<i>Hebe</i> spp.	Plantaginaceae	Raabe 1957, 1985
<i>heliconiae</i> (syn. <i>cubense</i> race 3)	None	<i>Heliconia</i> spp. (heliconia)	Heliconiaceae	Waite 1963; Ploetz and Bentley 2001; Ploetz 2006a
<i>heliotropae</i>	None	<i>Heliotropium europaeum</i> (heliotrope)	Heliotropiaceae	Netzer and Weintal 1987
<i>koa</i>	None	<i>Acacia</i> spp. (koa)	Fabaceae	Gardner 1978; Gardner 1980
<i>laciniati</i>	None	<i>Solanum laciniatum</i>	Solanaceae	Pandotra et al. 1971
<i>lactucae</i> (syn. <i>lactucum</i>)	1 to 4	<i>Lactuca sativa</i> (lettuce)	Asteraceae	Motohashi et al. 1960; Matuo and Motohashi 1967; Hubbard and Gerik 1993; Fujinaga et al. 2001, 2003; Gilardi et al. 2017
<i>lagenariae</i> (syn. <i>lagenaria</i>)	None	<i>Lagenaria siceraria</i> syn. <i>L. vulgaris</i> (bottle gourd), <i>Cucurbita ficifolia</i> (figleaf gourd syn. malabar gourd), <i>C. maxima</i> (winter squash)	Cucurbitaceae	Matuo and Yamamoto 1965; Armstrong and Armstrong 1978a; Nomura 1992; Namiki et al. 1994
<i>lathyri</i>	None	<i>Lathyrus sativus</i>	Fabaceae	Bhide and Uppal 1948; Gordon 1965
<i>lavandulae</i>	None	<i>Lavandula x allardii</i> (lavander)	Lamiaceae	Garibaldi et al. 2015b; Ortu et al. 2018

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TABLE 1
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<i>Forma specialis</i>	Races	Host plants (common name) ^a	Host plant family	Original references for the description of diseases, <i>formae speciales</i> , races, and host plants ^b
<i>lentis</i>	1 to 8	<i>Lens culinaris</i> syn. <i>L. esculenta</i> (lentil)	Fabaceae	Vasudeva and Srinivasan 1952; Gordon 1965; Pouralibaba et al. 2016; Hiremani and Dubey 2018
<i>lilii</i>	None	<i>Lilium</i> spp. (lily)	Liliaceae	Imle 1940, 1942; Baayen et al. 1998
<i>lini</i>	Unclear	<i>Linum usitatissimum</i> (flax)	Linaceae	Bolley 1901; Snyder and Hansen 1940; Brayford 1996c; Kroes et al. 1999
<i>loti</i>	None	<i>Lotus corniculatus</i> (birdsfoot trefoil)	Fabaceae	Gotlieb and Doriski 1983; Wunsch et al. 2009
<i>luffae</i>	None	<i>Luffa aegyptiaca</i> (sponge gourd), <i>Cucumis melo</i> (melon syn. muskmelon)	Cucurbitaceae	Kawai et al. 1958; Armstrong and Armstrong 1978a
<i>lupini</i>	1 to 3	<i>Lupinus</i> spp. (lupine)	Fabaceae	Wollenweber and Reinking 1935; Snyder and Hansen 1940; Armstrong and Armstrong 1964
<i>lycopersici</i>	1 to 3	<i>Solanum lycopersicum</i> (tomato)	Solanaceae	Saccardo 1886; Bohn and Tucker 1939; Snyder and Hansen 1940; Alexander and Tucker 1945; Grattidge and O'Brien 1982
<i>matthioli</i> (syn. <i>mathioli</i> , <i>matthiolae</i>)	1 (syn. f. sp. <i>conglutinans</i> race 3) and 2 (syn. f. sp. <i>conglutinans</i> race 4)	<i>Matthiola incana</i> (stock)	Brassicaceae	Baker 1948; Armstrong and Armstrong 1952; Bosland and Williams 1987
<i>medicaginis</i>	None	<i>Medicago sativa</i> (alfalfa)	Fabaceae	Weimer 1927, 1928; Snyder and Hansen 1940
		<i>Asparagus officinalis</i> (asparagus)	Asparagaceae	Armstrong and Armstrong 1969
<i>melongenae</i>	None	<i>Solanum melongena</i> (eggplant)	Solanaceae	Matuo and Ishigami 1958; Armstrong and Armstrong 1969
<i>melonis</i>	0, 1, 2, 1.2Y, 1.2W (previously 1 to 4)	<i>Cucumis melo</i> (melon syn. muskmelon)	Cucurbitaceae	Leach and Currence 1938; Snyder and Hansen 1940; Risser and Mas 1965; Risser et al. 1969, 1976
	1 to 7	<i>Cucumis melo</i> (melon syn. muskmelon)	Cucurbitaceae	Armstrong and Armstrong 1978a
<i>momordicae</i>	None	<i>Momordica charantia</i> (bitter gourd)	Cucurbitaceae	Sun and Huang 1983
<i>mori</i>	None	<i>Rubus</i> subgenus <i>Rubus</i> (blackberry)	Rosaceae	Gordon et al. 2016; Pastrana et al. 2017
<i>narcissi</i>	None	<i>Narcissus</i> spp. (narcissus)	Amaryllidaceae	Cooke 1887; Snyder and Hansen 1940; Linfield 1992
<i>nelumbicolum</i> (syn. <i>nelumbicola</i>)	None	<i>Nelumbo</i> sp. (lotus)	Nelumbonaceae	Nisikado and Watanabe 1953; Gordon 1965; Armstrong and Armstrong 1981

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TABLE 1
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<i>Forma specialis</i>	Races	Host plants (common name) ^a	Host plant family	Original references for the description of diseases, <i>formae speciales</i> , races, and host plants ^b
<i>niveum</i>	0 to 3	<i>Citrullus lanatus</i> (watermelon)	Cucurbitaceae	Smith 1894; Snyder and Hansen 1940; Cirulli 1972; Netzer and Dishon 1973; Netzer 1976; Zhou et al. 2010
		<i>Cucurbita pepo</i> (squash)	Cucurbitaceae	Martyn and McLaughlin 1983
<i>opuntiarum</i>	None	<i>Opuntia ficus-indica</i> (tuna cactus syn. spineless cactus), <i>Echinocactus grusonii</i> (golden barrel cactus), <i>Espostoa lanata</i> (peruvian old man cactus), <i>Schlumbergera truncata</i> (Thanksgiving cactus), <i>Ferocactus latispinus</i> (devil's tongue barrel cactus), <i>Mammillaria zeilmanniana</i> , <i>Astrophytum myriostigma</i> , <i>Cereus</i> spp.	Cactaceae	Pettinari 1951; Gordon 1965; Polizzi and Vitale 2004; Lops et al. 2013; Garibaldi et al. 2014, 2016; Bertetti et al. 2017
		<i>Euphorbia mammillaris</i>	Euphorbiaceae	Bertetti et al. 2017
<i>palmarum</i>	None	<i>Syagrus romanzoffiana</i> (queen palm), <i>Washingtonia robusta</i> (Mexican fan palm), <i>Phoenix canariensis</i> (Canary Island date palm), × <i>Butyagrus nabonnandii</i> (mule palm)	Arecaceae	Elliott et al. 2010, 2017; Elliott 2011
<i>papaveris</i>	None	<i>Papaver nudicaule</i> (iceland poppy)	Papaveraceae	Katan 1999; Garibaldi et al. 2012; Ortu et al. 2015b
		<i>Papaver</i> spp., <i>Chelinodium majus</i>	Papaveraceae	Bertetti et al. 2018
<i>passiflorae</i>	None	<i>Passiflora edulis</i> (passionflower), other <i>Passiflora</i> spp.	Passifloraceae	McKnight 1951; Gordon 1965; Gardner 1989
<i>perillae</i>	None	<i>Perilla frutescens</i> (perilla)	Lamiaceae	Kim et al. 2002
<i>pernicosum</i>	None	<i>Albizia julibrissin</i> (mimosa tree)	Fabaceae	Hepting 1939; Snyder et al. 1949
	1.2	<i>Albizia julibrissin</i> (race 1), <i>A. procera</i> (race 2)	Fabaceae	Toole 1952
<i>phaseoli</i>	1 to 7	<i>Phaseolus vulgaris</i> (common bean), <i>P. coccineus</i>	Fabaceae	Harter 1929; Kendrick and Snyder 1942a; Ribeiro and Hagedorn 1979; Woo et al. 1996; Alves-Santos et al. 2002
	27 races	<i>Phaseolus vulgaris</i>	Fabaceae	Henrique et al. 2015
<i>pisi</i>	1, 2, 5, 6 (up to 11 races before a revision of the race classification)	<i>Pisum sativum</i> (garden pea)	Fabaceae	Lindford 1928; Snyder 1933; Snyder and Hansen 1940; Schreuder 1951; Bolton et al. 1966; Haglund and Kraft 1970, 1979; Kraft and Haglund 1978
		<i>Cicer arietinum</i> (chickpea)	Fabaceae	De Curtis et al. 2014

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<i>Forma specialis</i>	Races	Host plants (common name) ^a	Host plant family	Original references for the description of diseases, <i>formae speciales</i> , races, and host plants ^b
<i>psidii</i>	None	<i>Psidium guajava</i> (guava)	Myrtaceae	Hayes 1945; Prasad et al. 1952; Pandey and Dwivedi 1985
<i>pyracanthae</i>	None	<i>Pyracantha</i> spp. (firethorn)	Rosaceae	McRitchie 1973; Armstrong and Armstrong 1981
<i>radicis-betae</i>	None	<i>Beta vulgaris</i> (sugar beet)	Amaranthaceae	Martyn et al. 1989; Harveson and Rush 1998; Hanson et al. 2018
<i>radicis-capsici</i>	None	<i>Capsicum annuum</i> , <i>C. chinense</i> (pepper)	Solanaceae	Lomas-Cano et al. 2014, 2016; Pérez-Hernández et al. 2014
<i>radicis-cucumerinum</i>	None	<i>Cucumis sativus</i> (cucumber), <i>C. melo</i> (melon syn. muskmelon), <i>Luffa aegyptiaca</i> (sponge gourd), <i>Citrullus lanatus</i> syn. <i>C. vulgaris</i> (watermelon), <i>Cucurbita pepo</i> (squash)	Cucurbitaceae	Vakalounakis 1996; Punja and Parker 2000; Vakalounakis et al. 2005; Cohen et al. 2015
<i>radicis-lupini</i>	None	<i>Lupinus</i> spp. (lupine)	Fabaceae	Weimer 1941, 1944
<i>radicis-lycopersici</i>	None	<i>Solanum lycopersicum</i> (tomato)	Solanaceae	Leary and Endo 1971; Jarvis and Shoemaker 1978
		<i>Solanum melongena</i> (eggplant)	Solanaceae	Rowe 1980
		Fabaceae spp.	Fabaceae	Rowe 1980; Menzies et al. 1990
		Cucurbitaceae spp.	Cucurbitaceae	Pirayesh et al. 2018
<i>radicis-vanillae</i> (syn. <i>vanillae</i>)	None	<i>Vanilla</i> spp. (vanilla)	Orchidaceae	Thomas 1918; Tucker 1927; Koyyappurath et al. 2015
<i>ranunculi</i>	None	<i>Ranunculus</i> sp. (buttercup)	Ranunculaceae	Garibaldi 1980; Garibaldi and Gullino 1985
<i>rapae</i>	None	<i>Brassica rapa</i>	Brassicaceae	Takeuchi and Kagawa 1996; Enya et al. 2008
<i>raphani</i> (syn. <i>conglutinans</i> race 2)	None	<i>Raphanus sativus</i> (radish), <i>Diplotaxis tenuifolia</i> (wild rocket), <i>Eruca vesicaria</i> syn. <i>sativa</i> (rocket salad)	Brassicaceae	Kendrick and Snyder 1942b; Bosland and Williams 1987; Garibaldi et al. 2006
<i>rauvolfii</i>	None	<i>Rauvolfia serpentina</i>	Apocynaceae	Janardhanan et al. 1964
<i>rhois</i> (syn. <i>callistephi</i> race 3)	None	<i>Rhus typhina</i> (staghorn sumac)	Anacardiaceae	Toole et al. 1948; Toole 1949; Snyder et al. 1949; Armstrong and Armstrong 1981
<i>saffrani</i>	None	<i>Crocus sativus</i> (saffron)	Iridaceae	Palmero et al. 2014
<i>simmondsia</i>	None	<i>Simmondsia chinensis</i> (jojoba)	Simmondsiaceae	Tsrer (Lahkim) and Erlich 1996; Tsrer (Lahkim) et al. 2007
<i>spinaciae</i>	1, 2	<i>Spinacia oleracea</i> (spinach), <i>Beta vulgaris</i> (beet)	Amaranthaceae	Hungerford 1923; Armstrong and Armstrong 1955a, 1976

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Races have been described in 25 of the 106 *formae speciales* described to date. These are *formae speciales* corresponding to plants of agronomic or ornamental interest. Although causality has not been demonstrated, it is difficult not to incriminate the role of humans in the current distribution and the emergence of new races within *formae speciales*. When interaction frequency between the host plant and the pathogenic *F. oxysporum* is low, as is the case with a few cultivated plants or plants not submitted to intensive cultivation, we may reasonably think that the first races that are described result from coevolution between

pathogenic *F. oxysporum* strains within a *forma specialis* and the host plant, therefore gene-for-gene relationships are expected. In view of the genetic selection done by breeders, it is more difficult to know if the newly cultivated genotypes act as accelerators of the evolution of phytopathogenic fungi or only reveal preexisting bypass genes that nothing could highlight otherwise. It is therefore clear that molecular markers are needed to unambiguously identify the races within *formae speciales* but also to understand the mechanisms of their emergence, even if this results in revising the initially defined gene-for-gene contours of the race concept.

TABLE 1
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<i>Forma specialis</i>	Races	Host plants (common name) ^a	Host plant family	Original references for the description of diseases, <i>formae speciales</i> , races, and host plants ^b
		<i>Silene chalconica</i> syn. <i>Lychnis chalconica</i> (Maltese cross)	Caryophyllaceae	Armstrong and Armstrong 1966b, 1976
<i>strigae</i>	None	<i>Striga hermonthica</i> , <i>S.</i> <i>asiatica</i> , <i>S. gesnerioides</i> (witchweed)	Orobanchaceae	Ciotola et al. 1995; Marley et al. 2005; Elzein et al. 2008
<i>tracheiphilum</i>	1 to 4	<i>Vigna unguiculata</i> (cowpea), <i>Glycine max</i> (soybean)	Fabaceae	Smith 1895; Snyder and Hansen 1940; Armstrong and Armstrong 1950; Hare 1953; Armstrong and Armstrong 1965a, 1968; Smith et al. 1999
		<i>Chrysanthemum x</i> <i>morifolium</i> (chrysanthemum), <i>Gerbera jamesonii</i> (gerbera)	Asteraceae	Armstrong and Armstrong 1965b; Troisi et al. 2010
<i>trifolii</i>	None	<i>Trifolium</i> spp. (clover)	Fabaceae	Jaczewski 1917; Bilai 1955; Gordon 1965; Pratt 1982
<i>tuberosi</i>	None	<i>Solanum tuberosum</i> (potato)	Solanaceae	Wollenweber 1916; Smith and Swingle 1904; Snyder and Hansen 1940; Manici and Cerato 1994
<i>tulipae</i>	None	<i>Tulipa</i> spp. (tulip)	Liliaceae	Apt 1958a, b; Baayen et al. 1998
<i>vasinfectum</i>	1, 2, 3, 4, 6, 8	<i>Gossypium</i> spp. (cotton), <i>Abelmoschus</i> <i>esculentus</i> syn. <i>Hibiscus</i> <i>esculentus</i> (okra)	Malvaceae	Atkinson 1892; Fahmy 1927; Armstrong et al. 1942; Armstrong and Armstrong 1958b, 1960, 1978b; Ibrahim 1966; Chen et al. 1985; Nirenberg et al. 1994; Cianchetta and Davis 2015
		<i>Senna</i> sp. syn. <i>Cassia</i> <i>tora</i> , <i>Medicago</i> sp. (alfalfa), <i>Glycine</i> sp. (soybean), <i>Nicotiana</i> sp. (tobacco), <i>Physalis</i> <i>alkekengi</i> , <i>Tithonia</i> <i>rotundifolia</i> (Mexican sunflower)	Fabaceae, Solanaceae, Asteraceae	Armstrong et al. 1942; Armstrong and Armstrong 1954b, 1958b, 1959, 1960, 1969
<i>voandzeiae</i>	None	<i>Vigna subterranea</i> syn. <i>Voandzeia subterranea</i> (bambarra groundnut)	Fabaceae	Ebbels and Billington 1972; Armstrong et al. 1975
<i>zingiberi</i>	None	<i>Zingiber officinale</i> (ginger)	Zingiberaceae	Trujillo 1963; Armstrong and Armstrong 1968; Stirling 2004

HOW TO DESCRIBE A NEW *FORMA SPECIALIS* OR RACE?

The *forma specialis* is not a taxonomic rank, therefore the nomenclature of *formae speciales* is not codified by the International Code of Nomenclature for algae, fungi and plants (Art. 4 Note 4). In other words, the definition of a new *forma specialis* does

not follow the rules of nomenclature established by the International Code of Nomenclature for algae, fungi and plants. Any author describing a new *forma specialis* is free to choose its name. As a result, many *formae speciales* were named according to the host plant Latin name, either the genus name or the species name, or according to the host plant common name (Table 1). The lack of any standardized nomenclature causes confusion in the definition of

TABLE 2
Insufficiently documented *Fusarium oxysporum formae speciales*

<i>Forma specialis</i>	Host plants (common name) ^a	Host plant family	References ^b	Comments
<i>adzuki</i>	<i>Glycine max</i>	Fabaceae	John et al. 2010	Insufficiently documented <i>forma specialis</i>
<i>aleuritidis</i>	<i>Vernicia fordii</i> (tungoil tree)	Euphorbiaceae	Suelong 1981	Insufficiently documented <i>forma specialis</i>
<i>amaranthi</i>	<i>Amaranthus hybridus</i> (amaranth)	Amaranthaceae	Chen and Swart 2001; Leslie and Summerell 2006	Insufficiently documented <i>forma specialis</i>
<i>barbati</i>	<i>Dianthus barbatus</i> (sweet William)	Caryophyllaceae	Snyder 1941; Armstrong and Armstrong 1954; Gordon 1965; Baayen et al. 1997	Possible confusion with <i>F. redolens</i> f. sp. <i>barbati</i>
<i>blasticola</i>	Conifers	Several families	Bilai 1955; Gordon 1965	Synonym of <i>forma specialis pini</i> according to Gordon 1965
<i>coffeeae</i>	<i>Coffea arabica</i> (coffee)	Rubiaceae	Garcia 1945	Insufficiently documented <i>forma specialis</i>
<i>coriandrii</i>	<i>Coriandrum sativum</i> (coriander)	Apiaceae	Narula and Joshi 1963; Koike and Gordon 2005	Insufficiently documented <i>forma specialis</i>
<i>cucurbitacearum</i>	<i>Cucurbitaceae</i> spp.	Cucurbitaceae	Gerlagh and Blok 1988	Gerlagh and Blok (1988) proposed to group together all the <i>formae speciales</i> pathogenic to plants from the family Cucurbitaceae
<i>dahliae</i>	<i>Dahlia</i> sp. (dahlia)	Asteraceae	Solovjova and Madumarov 1969; Armstrong and Armstrong 1981	Insufficiently documented <i>forma specialis</i>
<i>dioscoreae</i>	<i>Dioscorea rotundata</i> (yam)	Dioscoreaceae	Wellman 1972	Insufficiently documented <i>forma specialis</i>
<i>elaeagni</i>	<i>Elaeagnus</i> sp.	Elaeagnaceae	Armstrong and Armstrong 1968	Insufficiently documented <i>forma specialis</i>
<i>eleocharidis</i>	<i>Eleocharis dulcis</i> syn. <i>tuberosa</i> (Chinese water chestnut)	Cyperaceae	Donghua et al. 1988	Insufficiently documented <i>forma specialis</i>
<i>erucae</i>	<i>Eruca vesicaria</i> syn. <i>sativa</i> (rocket salad)	Brassicaceae	Chatterjee and Rai 1974; Garibaldi et al. 2003, 2006	The wilt of <i>Eruca vesicaria</i> could be caused by <i>F. oxysporum</i> f. sp. <i>raphani</i>
<i>freesia</i>	<i>Freesia</i> sp.	Iridaceae	Baayen et al. 2000; Taylor et al. 2016	Misidentification of two strains of f. sp. <i>gladioli</i> isolated from <i>Freesia</i>
<i>gerberae</i>	<i>Gerbera jamasonii</i> , hybrids (gerbera)	Asteraceae	von Arx 1952; Gordon 1965	Insufficiently documented <i>forma specialis</i>
<i>herbemontis</i>	<i>Vitis</i> spp. (grape)	Vitaceae	Tochetto 1954; Gordon 1965	Insufficiently documented <i>forma specialis</i>
<i>hyacinthi</i>	<i>Hyacinthus</i> sp. (hyacinth)	Asparagaceae	Muller 1978; Baayen et al. 2001	Possible confusion with <i>F. hostae</i>
<i>iridacearum</i>	<i>Iridaceae</i> spp.	Iridaceae	Roebroek 2000; Palmero et al. 2014	Roebroek (2000) proposed to group together all the <i>formae speciales</i> pathogenic to plants from the family Iridaceae

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^a According to the Integrated Taxonomic Information System (ITIS).

^b Supplementary File S2 provides a complete list of the references listed in this table.

formae speciales. Thus, some *formae speciales* have multiple names, e.g., the *forma specialis matthioli* also named *mathioli* or *matthiolae*. Any description of a new *forma specialis* or race should only be published after a meticulous search in the literature to avoid any duplicate entry. Moreover, pathogenicity should be evaluated in such conditions that the full pathogenic potentiality of the fungal

isolate is expressed, i.e., controlled conditions, nonexcessive inoculum dose and clearly identified susceptible cultivar. We suggest that proposing a new *forma specialis* or race should require the following at a minimum:

- Morphological and molecular identifications of the new isolate at the species level.

TABLE 2
(Continued from previous page)

<i>Forma specialis</i>	Host plants (common name) ^a	Host plant family	References ^b	Comments
<i>magnoliae</i>	<i>Magnolia</i> sp.	Magnoliaceae	Lin and Chen 1994	Insufficiently documented <i>forma specialis</i>
<i>nicotianae</i>	<i>Nicotiana tabacum</i> (tobacco), <i>Ipomoea batatas</i> (sweet potato)	Solanaceae, Convolvulaceae	Johnson 1921; Snyder and Hansen 1940; Clark et al. 1998; Rodriguez-Molina et al. 2013	<i>F. oxysporum</i> causes wilt of tobacco but the existence of the <i>forma specialis</i> <i>nicotianae</i> is debated among scientists
<i>orthoceras</i>	<i>Orobancha</i> sp. (broomrape)	Orobanchaceae	Wollenweber 1917; Snyder and Hansen 1940; Bilai 1955; Gordon 1965; Bedi 1994; Thomas et al. 1998	<i>F. orthoceras</i> was a synonym of <i>F. oxysporum</i> in early classifications of <i>Fusarium</i> . Some <i>F. oxysporum</i> strains are pathogenic to <i>Orobancha</i> spp. but the corresponding <i>forma specialis</i> is insufficiently described
<i>phormii</i>	<i>Phormium tenax</i> (New Zealand flax)	Xanthorrhoeaceae	Wager 1947	Insufficiently documented <i>forma specialis</i>
<i>physali</i>	<i>Physalis peruviana</i> (cape gooseberry)	Solanaceae	Simbaqueba 2017	Insufficiently documented <i>forma specialis</i>
<i>pini</i>	<i>Pinus</i> spp. (pine)	Pinaceae	Hartig 1892; Ten Houten 1939; Snyder and Hansen 1940; Matuo and Chiba 1966; Gordon et al. 2015	Insufficiently documented <i>forma specialis</i> . Possible confusion with <i>F. subglutinans</i> f. sp. <i>pini</i> , or <i>F. commune</i>
<i>querci</i>	<i>Quercus</i> sp. (oak)	Fagaceae	Georgescu and Mocanu 1956; Gordon 1965	Insufficiently documented <i>forma specialis</i>
<i>quitoense</i>	<i>Solanum quitoense</i> (naranjilla)	Solanaceae	Ochoa et al. 2001; Ochoa et al. 2004	Insufficiently documented <i>forma specialis</i>
<i>ricini</i>	<i>Ricinus communis</i> (castor bean)	Euphorbiaceae	Gordon 1965	Insufficiently documented <i>forma specialis</i>
<i>rosellae</i>	<i>Hibiscus sabdariffa</i> (roselle)	Malvaceae	Ooi and Salleh 1999; Ploetz et al. 2007	Insufficiently documented <i>forma specialis</i>
<i>sansevieriae</i>	<i>Sansevieria cylindrica</i>	Asparagaceae	Gupta et al. 1982	Insufficiently documented <i>forma specialis</i>
<i>sedi</i>	<i>Sedum</i> sp.	Crassulaceae	Raabe 1960	Insufficiently documented <i>forma specialis</i>
<i>sesami</i>	<i>Sesamum indicum</i> (sesame)	Pedaliaceae	Castellani 1950	Insufficiently documented <i>forma specialis</i>
<i>sesbaniae</i>	<i>Sesbania sesban</i> syn. <i>S. aegyptiaca</i>	Fabaceae	Singh 1956	Insufficiently documented <i>forma specialis</i>
<i>stachydis</i>	<i>Stachys sieboldii</i>	Lamiaceae	Jotani 1953; Gordon 1965	Insufficiently documented <i>forma specialis</i>
<i>tabernaemontanae</i>	<i>Tabernaemontana divaricata</i> syn. <i>T. coronaria</i>	Apocynaceae	Pande and Rao 1990	Insufficiently documented <i>forma specialis</i>
<i>tanaceti</i>	<i>Tanacetum parthenium</i> (feverfew)	Asteraceae	Hirooka et al. 2008	Insufficiently documented <i>forma specialis</i>
<i>vanillae</i>	<i>Vanilla</i> spp. (vanilla)	Orchidaceae	Thomas 1918; Tucker 1927; Gordon 1965; Koyyappurath et al. 2015	Renamed as f. sp. <i>radicis-vanillae</i>
<i>vasconcella</i>	<i>Carica x heilbornii</i> (babaco)	Caricaceae	Ochoa et al. 2000, 2004	Insufficiently documented <i>forma specialis</i>

- A full description of the protocol used for validating Koch's postulates, including the protocol and results of the pathogenicity test(s) together with the observed symptoms.
 - Evaluation of the specificity of the interaction between the new pathogenic strain and the host plant, and characterization of the host spectrum of the strain; appropriate crops to include would be those in the same plant family and/or grown in rotation with the known susceptible host.
 - The name of the new *forma specialis* according to the host plant Latin name when possible.
 - The race number according to the chronological order of discovery, and the identified virulence gene, if any.
- The accepted Latin binomial name of the host plant and the identified resistance gene, if any.
 - The names of one or more cultivars that have been demonstrated to be susceptible, along with differential cultivars where races have been described. Ideally, these are publicly available cultivars.
 - The deposition of representative isolates in an international collection of microorganisms.
 - The preservation of the host plant germplasms in an international collection, especially when a new race is described.
 - Publication in a peer-reviewed journal including all the biological details and providing the accession numbers in the text.

TABLE 3
***Fusarium oxysporum* host plants for which no *forma specialis* has been described**

Host plants (common name) ^a	Host plant family	Symptoms	References ^b
<i>Actinotus helianthi</i> (flannel flower)	Apiaceae	Wilt	Bullock et al. 1998
<i>Aloe vera</i> syn. <i>A. barbadensis</i> (Barbados aloe)	Xanthorrhoeaceae	Root and crown rot	Vakalounakis et al. 2015
<i>Alstroemeria</i> spp. (lily of the Incas)	Alstroemeriaceae	Wilt	Shanmugam et al. 2007
<i>Anemone</i> sp. syn <i>Pulsatilla koreana</i> (pasqueflower)	Ranunculaceae	Root rot	Su and Fu 2013
<i>Astrophytum ornatum</i>	Cactaceae	Wilt	Quezada-Salinas et al. 2017
<i>Bougainvillea glabra</i> (paper flower)	Nyctaginaceae	Wilt	Polizzi et al. 2010a
<i>Carya cathayensis</i> (Chinese hickory)	Juglandaceae	Rot	Zhang et al. 2015
<i>Chrozophora tinctorial</i> (turnsole)	Euphorbiaceae	Wilt	Trapero-Casas and Kaiser 1998
<i>Cichorium endivia</i> (endive)	Asteraceae	Wilt	Garibaldi et al. 2009
<i>Cladrastis kentukea</i> (yellowwood)	Fabaceae	Wilt	Graney et al. 2017
<i>Coleus forskohlii</i>	Lamiaceae	Wilt	Zheng et al. 2012
<i>Coreopsis verticillata</i>	Asteraceae	Wilt	Elmer et al. 2007
<i>Cucurbita pepo</i> (zucchini)	Cucurbitaceae	Wilt	Park et al. 2015
<i>Cymbidium</i> spp.	Orchidaceae	Root and stem rot	Benyon et al. 1996; Yao et al. 2018
<i>Daphne</i> sp.	Thymelaeaceae	Wilt	Kim et al. 2005
<i>Daucus carota</i> (carrot)	Apiaceae	Wilt	Han et al. 2012
<i>Dendrobium</i> spp.	Orchidaceae	Wilt	Xiao et al. 2012; Zhang et al. 2017
<i>Eremophila</i> spp.	Scrophulariaceae	Wilt	Polizzi et al. 2010b
<i>Fallopia multiflora</i> (tuber fleeceflower, hasuo)	Polygonaceae	Wilt	Park et al. 2015
<i>Firmiana simplex</i> (Phoenix tree, Chinese parasol tree)	Malvaceae	Stem canker	Zhang et al. 2013
<i>Helichrysum</i> spp.	Asteraceae	Wilt	Summerell and Rugg 1992
<i>Hevea brasiliensis</i> (rubber tree)	Euphorbiaceae	Stem rot	Li et al. 2014
<i>Hoodia gordonii</i>	Apocynaceae	Wilt	Philippou et al. 2013
<i>Hosta</i> sp. (plantain lily)	Asparagaceae	Root and crown rot	Wang and Jeffers 2000
<i>Gastrodia elata</i>	Orchidaceae	Tuber rot	Zhao et al. 2017
<i>Glycyrrhiza</i> spp. (licorice)	Fabaceae	Rot, wilt	Cao et al. 2013; Abedi-Tizaki and Zafari 2014
<i>Gypsophila</i> spp.	Caryophyllaceae	Wilt	Werner and Irzykowska 2007
<i>Lavandula pubescens</i>	Lamiaceae	Wilt	Perveen and Bokhari 2010
<i>Lewisia</i> spp. (bitterroot)	Montiaceae	Wilt	Garibaldi et al. 2005; Gullino et al. 2015

(Continued on next page)

^a According to the Integrated Taxonomic Information System (ITIS).

^b Supplementary File S3 provides a complete list of the references listed in this table.

TOWARD MOLECULAR TOOLS TO IDENTIFY *F. OXYSPORUM FORMAE SPECIALES* AND RACES

The internal transcribed spacer (ITS) has been proposed as the barcode for fungal species identification (Seifert 2009). However, this DNA marker cannot identify all *Fusarium* species unequivocally (O'Donnell and Cigelnik 1997). The translation elongation factor 1- α (*TEF1*) and the DNA-directed RNA polymerase II largest subunit (*RPB1*) and second largest subunit (*RPB2*) are *Fusarium* phylogenetically informative *loci* and allow for species identification (O'Donnell et al. 2013, 2015). The *TEF1* locus is also informative at the intraspecific level and can be combined with others such as the ribosomal intergenic spacer to reveal the complex genetic diversity within *F. oxysporum* (Canizares et al. 2015; Edel-Hermann et al. 2012, 2015; Lecomte et al. 2016; O'Donnell et al. 2009; Ortu et al. 2018). Sequence resources are available in the *FUSARIUM-ID* database (<http://isolate.fusariumdb.org/guide.php>; Geiser et al. 2004; Park et al. 2011) and the *Fusarium* MLST database (<http://www.westerdijkinstituut.nl/fusarium/>; O'Donnell

et al. 2010). The literature about *F. oxysporum* genetic diversity is very abundant. Studies are based on the use of various molecular tools that have evolved over time, as well as on the use of vegetative compatibility groups (VCGs) that group together genetically similar strains (Puhalla 1985). The number of VCGs in a given *forma specialis* is generally between 1 and 10, but can be up to 24 as in *forma specialis cubense* (Aguayo et al. 2017; Katan 1999; Kistler et al. 1998).

F. oxysporum diversity studies aim at identifying specific *forma specialis* markers to design diagnostic tools (Lievens et al. 2008). Many *formae speciales* are known to be polyphyletic, making it difficult to identify specific molecular markers (Baayen et al. 2000; Epstein et al. 2017; Fourie et al. 2009; Hill et al. 2011; Koyyappurath et al. 2015; O'Donnell et al. 1998, 2009). Additionally, soilborne and endophytic nonpathogenic *F. oxysporum* isolates can be highly variable genetically and closely related to pathogenic ones (Baayen et al. 2000; Edel et al. 2001; Fourie et al. 2009; Imazaki and Kadota 2015; Inami et al. 2014). One approach used to identify molecular markers of *F. oxysporum formae speciales* or races relies on insertion

TABLE 3
(Continued from previous page)

Host plants (common name) ^a	Host plant family	Symptoms	References ^b
<i>Limonium sinuatum</i> (statice)	Plumbaginaceae	Wilt	Taylor et al. 2017
<i>Mandevilla</i> (syn. <i>Dipladenia</i>) sp.	Apocynaceae	Wilt	Sella et al. 2010
<i>Medinilla myriantha</i>	Melastomataceae	Stem rot	Hernández-Lauzardo et al. 2018
<i>Miscanthus x giganteus</i>	Poaceae	Rhizome rot	Beccari et al. 2010
<i>Pandanus utilis</i> (screwspine)	Pandanaceae	Leaf spot	Guo et al. 2016
<i>Paris polyphylla</i> (Rhizoma Paridis)	Melanthiaceae	Stem rot	Zhou et al. 2018
<i>Phalaenopsis</i> spp.	Orchidaceae	Wilt	Kim et al. 2006
<i>Philodendron hederaceum</i> var. <i>oxycardium</i> (syn. <i>P. oxycardium</i>)	Araceae	Stem rot	Wang et al. 2016
<i>Plantago ovata</i> (desert Indianwheat)	Plantaginaceae	Wilt	Russell 1975
<i>Plukenetia volubilis</i> (Sacha Inchi)	Euphorbiaceae	Root and stem rot	Chai et al. 2018
<i>Portulaca molokiniensis</i> (ihi)	Portulacaceae	Stalk and root rot	Ma et al. 2018
<i>Protea</i> spp.	Proteaceae	Wilt	Swart et al. 1999
<i>Prunus avium</i> (sweet cherry)	Rosaceae	Root and crown rot	Úrbez-Torres et al. 2016
<i>Pseudotsuga menziesii</i> (Douglas-fir)	Pinaceae	Damping off	Bloomberg 1971; Stewart et al. 2012
<i>Pterocarpus angolensis</i>	Fabaceae	Wilt	Pearce 1979
<i>Rheum</i> sp. (rhubarb)	Polygonaceae	Leaf blight	Thakur et al. 2015
<i>Rhus aromatica</i> (fragrant sumac), <i>R. trilobata</i> (skunkbush sumac)	Anacardiaceae	Wilt	O'Mara and Tisserat 1997
<i>Rosmarinus officinalis</i> (rosemary)	Lamiaceae	Wilt	Ashrafi et al. 2010
<i>Saccharum</i> sp. (sugarcane)	Poaceae	Foliar disease	Bao et al. 2016
<i>Salvia sclarea</i> (clary sage)	Lamiaceae	Seedling disease	Subbiah et al. 1996
<i>Sanguinaria canadensis</i> (bloodroot)	Papaveraceae	Crown rot	Elmer and Marra 2012
<i>Smallanthus sonchifolius</i> (yacon potato)	Asteraceae	Root rot	Moraes et al. 2017
<i>Solanum aculeatissimum</i> syn. <i>S. khasianum</i> (nightshade)	Solanaceae	Wilt	Bordoloi et al. 1972
<i>Tectona grandis</i> (teak)	Lamiaceae	Wilt	Borges et al. 2018
<i>Torreya grandis</i>	Taxaceae	Crown and root rot	Zhang et al. 2016
<i>Trigonella foenum-graecum</i> (fenugreek)	Fabaceae	Wilt	Shivpuri and Bansal 1987
<i>Vaccinium corymbosum</i> (blueberry)	Ericaceae	Wilt	Liu et al. 2014
<i>Ziziphium jujuba</i>	Rhamnaceae	Rot	Rao 1964

sites of transposable elements; it provided specific detection tools for *formae speciales albedinis* and *lactucae*, among others (Fernandez et al. 1998; Pasquali et al. 2007). In other cases, random amplified polymorphic DNA allowed researchers to identify sequence-characterized amplified region (SCAR) markers. Following this strategy, detection tools were developed for *formae speciales basilici*, *cyclaminis*, *phaseoli*, *eustomae*, *cucumerinum*, and *radicis-cucumerinum* (Alves-Santos et al. 2002; Chiocchetti et al. 2001; Lecomte 2016; Li et al. 2010; Lievens et al. 2007). A few SCAR primers specifically detected races, e.g., in *formae speciales ciceri* and *melonis* (Jiménez-Gasco and Jiménez-Díaz 2003; Luongo et al. 2012).

Molecular identification of *F. oxysporum formae speciales* would ideally target pathogenicity-related genes. Although knowledge on these genetic determinants was scarce until recently, it has considerably improved in the last decade. One of the first such tools was developed for the *forma specialis lycopersici*, based on a host-specific virulence gene (Rep et al. 2004; Lievens et al. 2009). The gene encodes a small protein secreted in the xylem (SIX) which confers virulence to the fungus. Fourteen SIX genes are currently known, and a few homologs were found in other *formae speciales* such as *cepaе*, *cubense*, and *conglutinans* (Fraser-Smith et al. 2014; Li et al. 2016; Taylor et al. 2016; van Dam et al. 2016). PCR primers were designed from SIX sequences to discriminate the *formae speciales cubense* and *lycopersici* from other *formae speciales* (Fraser-Smith et al. 2014; Lievens et al. 2009). Molecular markers based on other virulence factors were also designed for *forma specialis phaseoli* and for race 4 of *forma specialis cubense* (Aguayo et al. 2017; Sousa et al. 2015). Apart from effector genes, other genes involved in *F. oxysporum* pathogenicity have been described as genes encoding cell wall-degrading enzymes or transcriptional regulators (Jonkers et al. 2009; Michielse et al. 2009a, 2009b). However, comparative genomics is the next step to identify host specificity in *F. oxysporum*. van Dam et al. (2016) performed whole genome sequencing of 45 *F. oxysporum* strains and managed to differentiate *formae speciales cucumerinum*, *niveum*, *melonis*, *radicis-cucumerinum*, and *lycopersici* on the basis of their effector pattern. Two years later, van Dam et al. (2018) designed PCR primers to discriminate the seven *formae speciales* that affect Cucurbitaceae based on candidate effectors extracted from 82 genome assemblies. There is no doubt that the expanding access to whole-genome sequences will continuously improve *F. oxysporum* host range identification.

SUMMARY AND FUTURE PROSPECTS

Many authors admit that the number of *F. oxysporum formae speciales* and races described in the review of Armstrong and Armstrong (1981) is out of date and suggest various and unfounded estimates of this number in the introduction of many papers dealing with *F. oxysporum*. More than the need to correct these estimates, the concomitant evolution of knowledge about the ecology of this complex species, the economic importance of its pathogenic/nonpathogenic activity, the development of tools—especially molecular-based genomic tools—to study it, and the redefinition of the concepts related to its characterization motivated our study and led us to revisit the literature on *F. oxysporum* in depth. Our analysis reveals that to date, 106 *formae speciales* have indeed been clearly described within *F. oxysporum*, and among these, 25 harbor from 2 to 24 races. However, these numbers are not definitive and are likely to change very soon for several reasons. The first reason is that 37 putative *formae speciales* have been described, but their characterization is insufficient to assert that they are indeed *formae speciales*, and 58 additional host plants have been reported. The second reason is related to the fact that studies have mainly focused on the pathogenic activity of *F. oxysporum* on plants of economic interest, but many uncultivated (wild) plants can also be infected by new *formae speciales* that remain to be described. Considering the proven

numbers of *formae speciales* and *formae speciales* hosting races provided by Armstrong and Armstrong (1981) (79 and 16, respectively) and those given by our study (106 and 25, respectively), the relative proportion of *formae speciales* hosting races has increased slightly. This increase might reflect a somewhat worrisome trend, as more and more new races are described within *formae speciales* in connection with the re-emergence of diseases on market gardening and ornamental crops but also on large scale crops, such as banana Fusarium wilt caused by race TR4 of *F. oxysporum* f. sp. *cubense* (Gilardi et al. 2017; Ploetz 2015; Zhou et al. 2010).

Greater diversity in *F. oxysporum* and within *formae speciales* may be revealed over time by using new plant genotypes derived from breeding. However, it is difficult to rule out, although not yet demonstrated, the role of mutagenic factors related to intensive culture conditions in the emergence of new diseases caused by *F. oxysporum*. Local appearance of race 3 from race 2 population within *F. oxysporum* f. sp. *lycopersici* in California underlines such possibility (Cai et al. 2003). The frequency of the occurrence of horizontal gene transfer as a factor of the evolution of *F. oxysporum* pathogenicity is not known but is probably low. However, given the natural inoculum density of this fungus in the soil and rhizosphere of many plants around the world, the process may not be anecdotal and may thus contribute to the emergence of new diseases caused by *F. oxysporum*, whether new *formae speciales* or new races within these *formae speciales*.

What farmers need most is early diagnostic tools. For some soilborne diseases, quantifying the infectious potential of soils helps to decide whether or not growing the host plant is possible. These measures are not applicable in the case of diseases caused by *F. oxysporum* (Alabouvette et al. 2006). This is why molecular tools to detect the presence and activity of pathogenic *F. oxysporum* isolates are needed. These tools must be able to discriminate between races and *formae speciales*, but also to distinguish them from nonpathogenic forms that are putative biocontrol agents. Recent comparative analysis of *F. oxysporum* genomes provided information on the genome organization and on the genomic region that governs pathogenicity (Ma et al. 2010, 2013). Genomic comparison of whole *formae speciales* genomes revealed that the effector repertoire of each *forma specialis* likely determines host specificity (van Dam et al. 2016, 2018). Such studies provide promising insights into the diversity and evolution of *F. oxysporum* pathogenicity. Future large-scale projects aimed at sequencing whole *F. oxysporum* genomes will assuredly improve host range identification and disease management. By combining the promising progress of genomics in characterizing the pathogenic effectors of each *F. oxysporum forma specialis* and race, and the potential of molecular techniques that are constantly evolving, a concrete and feasible challenge will be to develop diagnostic tools to preventively detect the risk of infection by *F. oxysporum* for a given crop and then to take the appropriate measures.

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