XVI. EUCARPIA

Capsicum and Eggplant Meeting

KECSKEMÉT • HUNGARY • 12-14.SEPT.2016

in memoriam
Dr. Alain Palloix



PROCEEDINGS

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Eggplant resistance to bacterial wilt and to *Fusarium* wilt: Is there a link?

Marie-Christine Daunay[1], Jean Winoc Hennart[2], Sylvia Salgon[3], Jacques Dintinger[3]

[1] *INRA UR1052, Montfavet (84), France*

[2] *Vco, Ledenon (30), France*

[3] *CIRAD, Saint Pierre, Reunion Island (France)*

Abstract

INRA UR1052 maintains a germplasm collection of *S. melongena* and related species. The accessions of this collection that are described in the literature as resistant to *Ralstonia solanacearum*, agent responsible of bacterial wilt, were screened at plantlet stage against *Fusarium oxysporum* f.sp. *melongenae* on the basis of the number of leaves wilted and vessels browning. Results show that the panel of accessions tested display phenotypes ranging from fully resistant to fully susceptible to *Fusarium* wilt, with all intermediate resistance levels. Results are discussed on the basis of the complexity of resistance evaluation and of what is known in tomato about a link between resistances to both vascular diseases.

1. Introduction

Eggplant, *Solanum melongena* L., is susceptible to several vascular diseases of soil born origin, mainly *Verticillium dahliae* in cool temperate conditions, *Fusarium oxysporum* f.sp. *melongenae* in warm temperate conditions (sandy soils), and *Ralstonia solanacearum* in tropical and equatorial conditions. Resistances to each of these disease exist within the intraspecific and interspecific eggplant germplasm, although their genetic characteristics are variable. Fragmented experimental and literature information suggests the existence of some link(s) between resistances of eggplant, as well as of tomato, to these or other vascular diseases. By focusing on two pathosystems, eggplant on one side, *Fusarium* and bacterial wilt on the other side, our purpose is to investigate the possible relationship between eggplant resistances to both diseases. The first part is a literature based overview of the knowledge about the pathogens and eggplant resistances. Second part presents results obtained by testing with *F.o.* f. sp. *melongenae* a collection of eggplant genetic resources, chosen because described in the literature as resistant to bacterial wilt (BW). Results are then discussed in light of the genetic and functional information available for eggplant, and to a lesser extent, tomato.

2. Eggplant and wilts pathosystems

Eggplant - Fusarium wilt pathosystem

Resistance to *Fusarium* wilt is available in *S. melongena* germplasm (Abdullaeva & Shifman, 1988; Mandare & Patil, 1993; Sakata et al., 1996). A monogenic dominant control was identified in eggplant accessions -LS174, LS1934 and LS2436- [Sakata et al., 1996; Mochizuki et al., 1997; Mutlu et al., 2008; Boyaci et al., 2011). Miyatake et al. (2016)

positionned at the end of chromosome 2 the locus (*FM1*) two allelic forms of which were identified in LS174 ($Fm1^E$) and LS1934 ($Fm1^L$). Two closely linked SRAP and SRAP-RGA markers, mapped 1.2 cM from the LS2436 resistance gene were developed by Mutlu et al. (2008) for marker assisted selection. The locus responsible of the resistance of *S. melongena* LS2436 was mapped on the middle of eggplant chromosome 4, syntenic to tomato chr.4 (Miyatake et al., 2016)).

Resistance to *Fusarium* wilt was also found in several *Solanum* species related to eggplant such as *S. torvum*, *S. sisymbriifolium*, *S. aethiopicum*, *S. violaceum* and others (Yamakawa & Mochizuki, 1979; Cappelli et al;, 1995; Monma et al., 1996; Gousset et al., 2005; Boyaci et al., 2012). The genetic control of the resistance of two *S. aethiopicum* accessions belonging to cultigroups Aculeatum and Gilo, was shown as monogenic dominant, (Rizza et al., 2002; Toppino et al., 2008). Progenies derived from anther culture and interspecific somatic hybrids '*S. melongena* X *S. aethiopicum*' (Rotino et al., 2005) allowed Toppino et al. (2008) (i) to identify the locus *Rfo-sa1* which controls the resistance of *S. aethiopicum* to *Fusarium* wilt, as well as (ii) its two allelic forms, respectively specific to groups Aculeatum and Gilo. *Rfo-sa1* was positioned later on the eggplant Linkage Group 1 of Barchi et al. (2010). Miyatake et al. (2016) mapped *Rfo-sa1* very close to *FM1*.

All in all, three loci controlling *Fusarium* wilt resistance are identified today, two on *S. melongena* chromosome 2 (*FM1* and *Rfo-sa1*, with two allelic forms each) and one on chromosome 4 (Miyatake et al., 2016). So far, no interaction has been described between these loci and *Fusarium* strains, unlike monogenic resistances based on different mechanisms and controlling three *Fusarium* races in tomato (Gonzalez-Cendales, 2016). Further, in tomato polygenic tolerance has also been described (Crill et al., 1972).

Eggplant - bacterial wilt pathosystem

Resistance to BW, as in the case of *Fusarium* wilt, has been found in *S. melongena* germplasm. The resistances found in different accessions are described as dominant or recessive, monogenic or polygenic, depending on the accessions (compiled in Daunay, 2008). A first single dominant gene of resistance identified in the Chinese accession E-31, was marked with a SCAR marker distant from 3.33 cM (Cao et al., 2009). In this accession, the function of a putative BW resistance gene (the same ?), named *RE-bw*, was characterized, including its interaction with the bacterial *Popp2* avirulence factor (*Xiao Xi'ou* et al., 2015). Another major dominant gene, *Ers1*, probably positionned on chromosome 9 controls the resistance of the INRA accession AG91-25 (Lebeau et al., 2013); its interactions with *Ralstonia* type III effectors are under current research (Peeters et al., pers. comm.). *Ers-1* is escorted by a few QTLs, the efficiency of which depends on the bacterial strains used.

Resistances to BW have also been found in several *Solanum* species related to eggplant (Hébert, 1985; Clain et al., 2004; Gousset et al., 2005; Daunay, 2008), in particular in *S. torvum* , *S. aethiopicum*, *S. sisymbriifolium*, and *S. violaceum*, some of which are used as rootstocks for eggplant. This does not mean that all accessions of each of these species are resistant to all strains. For instance susceptibility or partial susceptibility of some accessions of *S. torvum* (Saito et al., 2010; Gousset et al., 2005) and *S. aethiopicum* (Hébert, 1985) is mentionned. Further, bacteria can be isolated from roots or lower stem of symptomless *S. torvum* (Clain et al., 2004; Gousset et al., 2005) which means that the resistance of this species, as in eggplant and tomato (Grimault & Prior, 1994), is an ability to limit the upward spread of the bacteria within xylem vessels.

The resistance of *S. aethiopicum* was transferred into *S. melongena* by sexual interspecific

crossing (Ano et al., 1991) as well as by protoplast fusion (Collonnier et al., 2001b). Somatic hybrids between *S. melongena* on one hand, and *S. torvum* (Collonnier et al., 2003b) or *S. sisymbriifolium* on the other (Collonnier et al., 2003a), as well as somatic hybrids between *S. integrifolium* (= *S. aethiopicum*) and *S. violaceum* (Tamura et al., 2002) are as resistant or less than their resistant parent.

The major trouble the breeders face for creating resistant material to BW is the unstability accross locations of the resistances they use, whatever the solanaceous crop they work with (Huet, 2014), because of biotic (complexity of the pathogenic process, interactions of the resistances with local bacterial strains, synergy with root knot nematodes), as well as abiotic reasons (influence of soil type and moisture, temperature and light intensity) (Hayward, 1991). In eggplant, as in tomato, the resistance is an ability to limit the spread of the bacteria within the stem xylem vessels (Grimault & Prior, 1994). This means that wilt is not a sufficient criteria for assessing resistance, and must be completed with a colonization index, as did Lebeau et al. (2011) who revealed the existence of compatible or incompatible interactions among a set of resistant accessions of both species. The wide genetic diversity of the thousands strains of *Ralstonia solanacearum* is another major impediment. The classification of the BW complex, initially based on host range (races), then on metabolic properties (biovars), has strongly evolved with the availability of molecular techniques, from which Sequevars, Clades, Phylotypes (Fegan & Prior, 2005) were defined. The numerous pathogenicity components of the bacteria have been reviewed by Peeters et al. (2013). New species have been defined recently within this complex (Prior et al., 2016). On the whole, all this means that research on resistance spectrum, genetic determinism and/or functional characterization needs intimate genetic knowledge of the bacterial strains used, as was shown in Lebeau et al. (2011). These authors exemplified the complexity of the interactions between a range of bacterial strains representative of the diversity of the bacteria, and a core collection of resistant genitors of three solanaceous crops (eggplant, tomato and pepper).

Resistance to several vascular diseases

Resistance to both *Fusarium* and bacterial wilts is mentionned in the literature for some eggplant accessions, such as LS1934 and LS 2436 (e.g. Sakata et al., 1996) as well as for several eggplant relatives such as *S. aethiopicum* Aculeatum and Gilo Groups, *S. torvum*, *S. sisymbriifolium* and *S. violaceum* (e.g. Narikawa et al., 1988; Collonnier et al., 2001a; Gousset et al., 2005; Daunay, 2008). However, the available data are limited in terms (i) of number of accessions tested for each *Solanum* species and (ii) fungal or bacterial strains used, although interactions between accessions and *Ralstonia solanacearum* strains exist. Such interactions could explain why some results even refute the link between both resistances, such as those of Monma et al. (1996) who found all their 53 *S. aethiopicum* accessions resistant to *Fusarium* wilt, being susceptible to BW.

Additional resistance to *Verticillium* wilt is described in the eggplant accession LS2436 (Sakata et al., 1996; Saito et al., 2010), as well as in some *S. torvum* accessions (Narikawa et al., 1988), which resist to the three vascular diseases.

Interestingly in tomato, association within single genotypes (such as the famous Hawaii 7996) of resistance to three vascular diseases, bacterial wilt, bacterial canker and *Fusarium* wilt race 2 (in the absence of gene I-2), has been noticed by Laterrot et al. (1978) and Laterrot & Kaan (1978).

Literature testifies that these « coincidences » (i.e. the resistance to two or three vascular diseases within a single gentotype) are not systematic, since they are found in a number of

accessions only, and not in all accessions resistant to the one or the other of these disease resistance examples.

The summing up presented above explains why, intrigued by these occasional (but frequent enough to stick curiosity) association of resistances to two or more vascular diseases, within single genotypes in eggplant, related *Solanum* species as well as tomato, we further tested the hypothesis of a putative link between the resistance to bacterial and *Fusarium* wilt, on a range of eggplant germplasm. The synteny between the genomes of eggplant and tomato,, and the growing knowledge of the genetic factors involved in the resistance to each of these diseases in both crops, provides a good background for unravelling in the future the possible genetic and functional similarities which could explain the presence in some accessions, of resistance to these two (or more) vascular diseases.

3. Screening of genetic resources

Material and methods

The INRA germplasm database was sorted out for identifying a sampling of *S. melongena* and related *Solanum* spp. accessions recorded as resistant to BW (**Table 1**). The behaviour « resistant » is a very « rough data », given bacterial wilt resistance is quantitative and depends on the bacterial strains tested. The information for resistance to BW originates either from INRA results obtained in the French West Indies, or from accessions donor, or from literature.

This material was tested to *Fusarium oxysporum* f. sp. *melongenae*. Susceptible controls were *S. melongena* Banaras Giant (MM 608) and Violette de Barbentane (LF3-24); Resistant controls were *S. aethiopicum* Aculeatum Group (MM 134) and *S. sisymbriifolium* (MM 284).The inoculation method is close to that used at INRA for tomato (Moretti & Laterrot, 1994). Inoculum was prepared by cultivating a Japanese *Fusarium* strain (TF 161), obtained from Takii France, on an agitated synthetic culture medium, 8 days at 10 hours day/14h night and 18/23°C. At the time of inoculation, the solution was grinded and filtered. Two dilutions were used, one $1/5^{th}$ in distilled water and $1/10^{th}$. Dilution $1/5^{th}$ matches 10^6 conidies/ml.

After sowing in pans, plantlets 18-21 days old were removed, roots are rinsed, partially cut, dipped into the inoculum for 5 mn and transplanted in new pans filled 2/3 compost, 1/3 sand (four accessions and one control -susceptible or resistant- per pan). Pans were then settled in a climatic chamber, regulated 12h/12h, 28°C constant. Twenty plants per genotype and per inoculum dilution were tested, given enough plantlets were available. Two weeks afer inoculation, symptoms were recorded on each plant as:

- resistant: no wilting, no vessels browing (or browning limited to hypocotyl),
- susceptible: wilting or no wilting, vessels browning present in the stem, further up cotyledons insertion.

Percentage of resistant plants was calculated as: 100 * [number of resistant plants / 20].

The test was repeated by Vilmorin in 2003, with two repeats of 7 seven plants per accession. The percentage of resistant plants was calculated on the basis of two measurements, foliar wilting and vessels browing (scales not shown).

Results

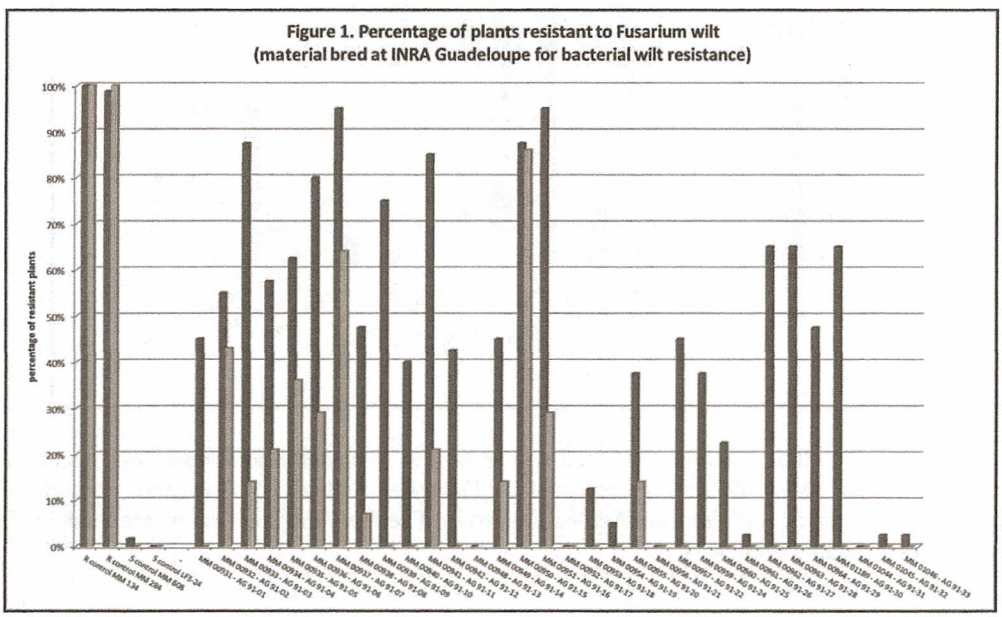
The inoculum dilution ($1/5^{th}$ or $1/10^{th}$), used in INRA screening test, did not affect the response of susceptible and resistant controls but some slight up or down variation of the proportion of susceptible and resistant plants was recorded for the accessions tested (data not shown). For the sake of clarity, we present the INRA results of both dilutions merged together. Further, as there was a close link between the two measurements used by Vilmorin - foliar wilting and vessels browing - (data not shown), we present only Vilmorin results on the basis of the percentage of resistant plants calculated from the vessels browning. Results are presented for the material subdivided into three categories. **Figure 1** is focused on AG-xx accessions, issued from BW breeding programs carried out at INRA Guadeloupe. **Figure 2** is focused on accessions of INRA *S. melongena* collection described as resistant to BW. **Figure 3** displays the results for a set of *Solanum* spp. also described as resistant to BW. All histograms display the results for both INRA and Vilmorin tests. For each accession tested, the left, dark grey, bar illustrates INRA results, and the right one, light grey, Vilmorin results.

Species	Accession number	Name or other number	Total number of plants tested (INRA)	Total number of plants tested (Vilmorin)
S. aethiopicum (Aculeatum group)	**R control MM 134**		60	41
S. sisymbriifolium	**R control MM 284**		80	56
S. melongena	**S control MM 608**	Giant of Banaras	60	63
S. melongena	**S control LF3-24**		70	68
S. melongena	MM 00931	AG 91-01	40	14
S. melongena	MM 00932	AG 91-02	40	14
S. melongena	MM 00933	AG 91-03	40	14
S. melongena	MM 00934	AG 91-04	40	14
S. melongena	MM 00935	AG 91-05	40	14
S. melongena	MM 00936	AG 91-06	40	14
S. melongena	MM 00937	AG 91-07	40	14
S. melongena	MM 00938	AG 91-08	40	14
S. melongena	MM 00939	AG 91-09	40	14
S. melongena	MM 00940	AG 91-10	40	14
S. melongena	MM 00941	AG 91-11	40	14
S. melongena	MM 00942	AG 91-12	40	14
S. melongena	MM 00948	AG 91-13	5	0
S. melongena	MM 00949	AG 91-14	40	14
S. melongena	MM 00950	AG 91-15	40	14
S. melongena	MM 00951	AG 91-16	40	14
S. melongena	MM 00952	AG 91-17	40	14
S. melongena	MM 00953	AG 91-18	40	14
S. melongena	MM 00954	AG 91-19	40	14
S. melongena	MM 00955	AG 91-20	40	14
S. melongena	MM 00956	AG 91-21	40	14
S. melongena	MM 00957	AG 91-22	40	14
S. melongena	MM 00959	AG 91-24	8	0
S. melongena	MM 00960	AG 91-25	40	14
S. melongena	MM 00961	AG 91-26	40	14
S. melongena	MM 00962	AG 91-27	40	14
S. melongena	MM 00963	AG 91-28	40	14
S. melongena	MM 00964	AG 91-29	40	14
S. melongena	MM 01189	AG 91-30	40	14
S. melongena	MM 01044	AG 91-31	40	14
S. melongena	MM 01045	AG 91-32	40	14
S. melongena	MM 01046	AG 91-33	40	14
S. melongena	MM 120	Nan Tan	40	0
S. melongena	MM 127	Turquie	40	14
S. melongena	MM 152	Ceylan SM 164	40	14
S. melongena	MM 165	Sinampiro	40	14
S. melongena	MM 412	Taiwan Naga	40	0
S. melongena	MM 413	n°1	40	14
S. melongena	MM 415	Mayon	40	14
S. melongena	MM 799	SM6	40	14
S. melongena	MM 853	Dingras Multiple Purple	40	14
S. aethiopicum (Aculeatum group)	MM 457		40	14
S. aethiopicum (Gilo group)	MM 196 TER		40	14
S. aethiopicum (Gilo group)	MM 229		40	14
S. aethiopicum (Gilo group)	MM 232 BIS		40	14
S. aethiopicum (Gilo group)	MM 283		40	14
S. aethiopicum (Gilo group)	MM 348		40	14
S. aethiopicum (Gilo group)	MM 854		40	14
S. aethiopicum (Gilo-anguivi group)	MM 236		40	14
S. aethiopicum (Kumba group)	MM 574		40	14
S. melongena gr E	MM 498		40	14
S. stramonifolium	MM 416		40	0
S. violaceum	MM 497		40	14
S. violaceum	MM 1027		40	14
S. virginianum	MM 265		40	14

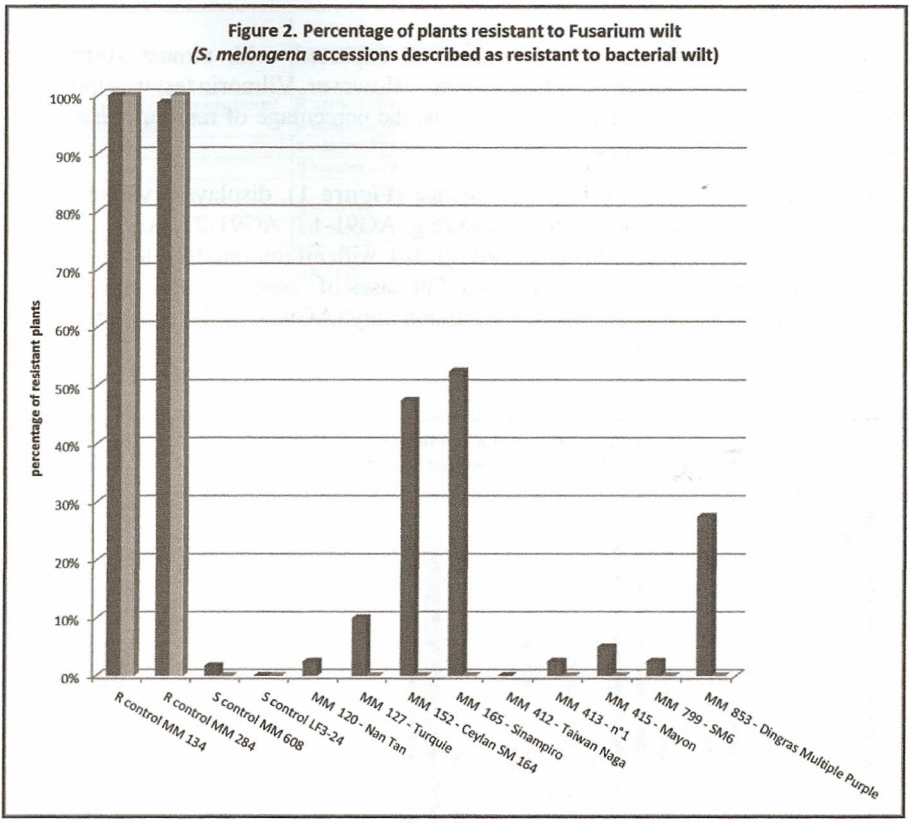
Table 1:
List of the eggplant germplasm resistant to bacterial wilt, tested for Fusarium wilt

Resistant and susceptible controls behaved as expected, with almost 100% of plants respectiveley healthy or dead, for both series of tests. However, Vilmorin test was more stringent than INRA test, since for all but a few accessions, the percentage of resistant plants is almost systematically lower (**Figures 1, 2, 3**).

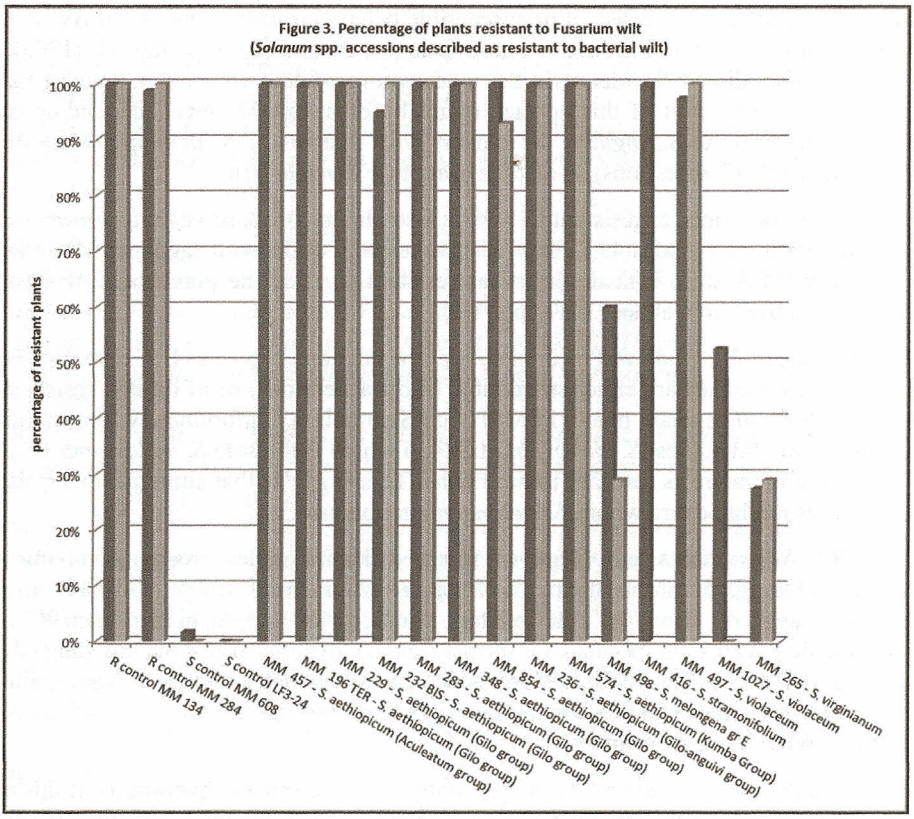
The material bred at INRA for BW resistance (**Figure 1**), displays a variable behaviour towards *Fusarium* wilt, from fully susceptible (e.g. AG91-17, AG91-21, AG91-31) to a high level of resistance in INRA test (AG91-07, AG91-16), with all intermediate levels of resistance between the extremes for the other accessions. For cases of resistance, resistance level is less than that of the resistant controls. For one accession only (AG91-15) the resistant behaviour is similar in both INRA and Vilmorin tests.



The set of *S. melongena* accessions described as resistant to BW, is overall susceptible to *Fusarium* wilt, although MM 152 and MM 165 are moderately susceptible with some 50% plants resistant (**Figure 2**).



Interestingly, all *S. aethiopicum* tested and as well as *S. stramonifolium* and one accession of *S. violaceum* (MM 497) are as resistant to *Fusarium* wilt as both resistant controls, *S. sisymbriifolium* and *S. aethiopicum* Aculeatum group. The few other accessions are moderately or slightly resistant (**Figure 3**).



4. Discussion and conclusion

Our experiments, carried out in 2002, suffer two limitations. First, they involve a material chosen on the basis of the (solely) rough/global information related to bacterial wilt resistance, although resistance to BW is complex in terms of (i) interactions between resistance progenitors and bacterial strains (Lebeau et al., 2011), (ii) of genetic controls (so far unravelled only for a very limited number of genotypes) as described in section 2, and (iii) of symptoms (unwilted plants can be severely colonized by the bacteria and environment changes can provoke their unexpected sudden wilting). Second, for the screening tests towards *Fusarium* wilt, we did not expect an heterogeneous behaviour within accessions, from one plant to another. This led to quantitative resistance levels (ranging between 0 and 100% resistant plants). Because of funding shortage, we could not check whether this heterogeneity was a matter of heterozygozity or of inoculum pressure.

Despite these limitations, our *Fusarium* wilt resistance screening tests of *S. melongena* accessions and *Solanum* spp. accessions bred for resistance to BW, or described as resistant, indicate, in some cases, the existence of a genotype-dependant association between the resistances to both wilts. The closer association is found in accessions of *S. aethiopicum* (**Figure 3**) as indicated by our results (9 accessions, described as resistant to BW, almost 100% resistant to *Fusarium* wilt) This association is found in the three cultigroups tested, Aculeatum (syn. *S. integrifolium*), Gilo and Kumba. However, these results contradict those of Monma et al. (1996) who found 100% of their 53 *S. aethiopicum* accessions resistant to *Fusarium* wilt, but susceptible to BW. These facts are clues that (i) resistance to *Fusarium* wilt is frequent in *S.*

aethiopicum and (ii) that the resistant or susceptible behaviour of this species to BW depends on the bacterial strains used. Further, the *Fusarium* wilt results of Cappelli et al. (1995), who found a 27 to 47% disease incidence in three accessions of *S. aethiopicum*, suggest that the resistance to *Fusarium* wilt of this species might be of a variable level, depending on the accessions. Interestingly, *S. anguivi*, the closest wild relative of *S. aethiopicum*, tested by Monma et al. (1996) (7 accessions), is also resistant to *Fusarium* wilt..

S. violaceum, described as resistant to BW, is also almost 100% resistant to *Fusarium* wilt, but for one accession only (MM 497) out of the two tested. For the wild eggplant (MM 498) and *S. virginianum* (MM 265), both described as resistant to BW, the percentage of *Fusarium* resistant plants varies from almost 30% up to 60%.

The incidence of *Fusarium* wilt on *S. melongena* accessions known as BW resistant (**Figure 2**) is important, since they are either susceptible (most accessions) or of limited resistance for the best one (50% of resistant plants in MM 165, Sinampiro). Unfortunately, but because of unavailability, we did not test *S. melongena* LS2436 which is the sole *S. melongena* accession described in the literature as resistant to both wilts. This suggests that simultaneous resistance to both diseases might be rare within *S. melongena* germplasm.

The INRA AG-xx accessions (**Figure 1**), issued from complex crosses involving many progenitors including, for most of them, *S. aethiopicum* Aculeatum Group (MM 134), display a variable percentage of *Fusarium* wilt resistant plants, from null to higher than 90%. The available data do not allow to speculate far further from the hypothesis that the breeding program carried out at INRA Guadeloupe for BW resistance, has somehow, and more or less, « diluted » the *Fusarium* wilt resistance(s) of *S. aethiopicum* and/or of the possible *Fusarium* wilt resistance of the other BW resistant progenitors.

Our results do not invalidate but do not validate either the starting hypothesis of this paper, about a possible link between resistances to *Fusarium* and bacterial wilts. This link, if existing, at least in some genotypes of eggplant and relatives as well as in tomato, could involve plant genes or QTLs involved in both resistances, or involve distinct genes inducing similar physiological reactions, or both. The existing synteny between both Solanaceous species, and the increasing knowledge of their genome provide tools for running cross search of the generalist ou pathogens-specific genes and mechanisms involved in controlling vascular diseases. Both diseases are vascular and induce the same kind of plant disorders, hence non specific plant defenses limiting these disorders probably exist. The root system and what happens at the cotyledons insertion point seem to play a key role in limiting the development and upward spread of the vascular pathogens, once entered within the roots xylem vessels. Hence, given (i) the developping knowledge of the genetic controls to both diseases, and of the structure and expression of *Fusarium* (e.g. Barbierato et al., 2016) and BW resistance genes (e.g. Reddy et al., 2015), as well as (ii) the ongoing better management of *Ralstonia solanacearum* strains (genotypes) used in resistance tests, promising studies are expected in a near future, aiming at a better understanding of the specific and/or common physiological and genetic mechanisms controlling the resistance to vascular wilts, including *Fusarium* and bacterial wilts.

Authors are thankful to Dr Ph. Prior (INRA-CIRAD, La Réunion) for reviewing this paper.

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