Origins of major genes for downy mildew resistance in sunflower

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ABSTRACT

New sources of major gene resistance to sunflower downy mildew were compared with known resistance genes. All genes appear to come from crosses with wild *Helianthus*, and most frequently from wild *H. annuus*. The gene *Pl6* has been found in many different ecotypes but resistances which segregate independently from this gene have also been obtained. Genes considered as different may be the result of intra-cluster recombinations. Only 1 or perhaps 2 genes have been obtained from *H. argophyllus*. Identification of genes from *H. tuberosus*, is not complete, possibly because these sources show downy mildew sporulation on cotyledons. Some other annual species also show major gene type resistances. It is concluded that knowledge of these sources is important, both for their use in breeding and also to distinguish between major gene and quantitative resistance.

Key words: introgression – *Pl* genes – *Plasmopara halstedii* – resistance tests – segregation.

INTRODUCTION

Over 40 years, there has been considerable search for new genes giving resistance to new downy mildew races when these appear. Well known genes have been shown to be clustered: firstly *Pl1, Pl2, Pl6* and *Pl7* (Mouzeyar et al., 1995; Roeckel-Drevet et al., 1997; Mestries et al., 1998) on LG 8 (Cartisol LG1), secondly *Pl5* and *Pl8* (Bert et al., 2001; Radwan et al., 2004), on LG13 (Cartisol LG6) and more recently *Plarg* (Dussle et al., 2004) on LG1 (CartisolLG13). The *Pl2/Pl6* cluster was found to have a structure TIR-NBS-LRR (Bouzidi et al., 2001), typical of specific resistance genes producing hypersensitive reactions whereas the *Pl5/Pl8* cluster was shown to be NBS-LRR-CC (Radwan et al., 2002). *Pl6* has been found to show within-gene segregation leading to separation of resistances to races 703 and 710 from those for races 100 and 304 (Vear et al., 1997). Many other ecotypes of wild *H. annuus* or other wild species, in particular *H. argophyllus* have been tested and resistances introgressed into cultivated sunflower. This requires a large effort, and before being able to say whether a gene is new, it is necessary to have the homozygous form, and then make crosses with known genes. So the question may be asked as what wild species give the greatest probability of finding new and useful genes. This paper compares origins in cultivated sunflower, wild *H. annuus* and *H. argophyllus* and some other species, both from the bibliography and from recent genetical analyses made by INRA.

MATERIALS AND METHODS

Material: All the cultivated sunflower lines: resistance sources, race differentials and susceptible lines used for test crosses are maintained by INRA, together with collections of wild *H. annuus* and other *Helianthu*s species, interspecific pools and introgressions. For genetical analyses, it was necessary for lines to be homozygous for downy mildew resistance and to produce sufficient seed for tests to be made with several downy mildew races. Test cross progenies were obtained by crossing new resistance sources with lines carrying known genes and then crossing the F_1 hybrid with a completely susceptible line. These progenies were then tested to determine whether they segregated for downy mildew resistance (no segregation: same gene or closely linked; 3R/1S: 2 independent genes).

Downy mildew resistance tests: Classic seedling tests on germinated seed (Tourvieille de Labrouhe et al., 2000) were carried out in growth chambers approved for manipulation of downy mildew races observed in France. Large scale tests, with 100-300 seedlings per progeny, to determine genetical segregation were made with races 710, 304, and 703. Test of resistance to other races were made on 20-30 plants/genotype, with races 100, 314, 334, 704 and 714.

RESULTS

Resistance sources: Table 1 presents knowledge of origins and *Pl* genes in the species most commonly used as resistance sources.

Resistance from cultivated sunflower: In these sources, resistance did not come directly from wild *Helianthus*. However, the ancestors reported suggest that downy mildew resistance came from crosses with wild species at some time, although there are some specificities that have not appeared in recent crosses. The lines nearly all appear to be traceable to a Canadian line 953 involving wild *H. annuus* (Fick and Zimmer, 1974), with crosses made either at Morden or by INTA in Argentina. *Pl1* came from 953-102-1-1, and was included in varieties such as Advent, from which Vrânceanu and Stoenescu (1970) obtained AD66, but also Rha265 and RHA266. *Pl2* came from both 953-102 giving RHA274, and 953-88 as HA61. *Pl2* was widely used, but new sources have not been reported, perhaps they have not been retained since they do not provide resistance to recent downy mildew races. Although partly from the same origin, downy mildew resistance from Argentinean populations appears quite specific because, at least in the resources held and lines developed at INRA, they are all resistant to race 710 but susceptible to race 703. According to the ancestry detailed by Romano and Vazquez (2003), resistance in the open pollinated variety Guayacan, and so the pool USDA HAR5 and INRA line QHP1, also came from the Canadian line 953-102. In contrast, resistance in the varieties Charata (which gave HAR4) and Caburé probably came from an Argentinean interspecific pool with Russian open pollinated varieties crossed with *H. annuus*, *H. argophyllus* and *H .petiolaris* in 1955/56. It seems likely that in the multiplication of these open pollinated varieties some intercrossing must have occurred, to have spread the gene which we refer to as "Pl_{QHP1}". In the development of the USDA or INRA lines, resistance to race 710 was certainly retained because that was the most useful resistance, but the combination with susceptibility to race 703 is quite specific and not known for any other resistance source. This resistance segregates as a single dominant gene, giving clear resistance; it also segregates in test crosses with *Pl6* (in spite of apparently having a common origin with *Pl1* and *Pl2)* and also *Pl5*, and *Plarg* (Table 1). Bulk segregant analyses have been made, but this gene has not yet been located on a linkage group.

Resistance directly from wild Helianthus annuus

(i) Pl6: Miller and Gulya (1991) developed HA335 and HA336 from crosses with wild *H. annuus* from Texas with resistance to all known races except those named "xx4", such as 304, 314 and 334, observed in France. Their resistance gene *Pl6* was located in the cluster with *Pl1* and *Pl2*. More recently, in collaboration with J. Miller, we found that 2 other USDA origins probably also carry *Pl6* (Table 1), both being resistance to race 710 and susceptible to race 304: "TP5", from a Californian *H. annuus* and HA459 (from a Texas *H. annuus)*. Some origins from crosses made at Montpellier, with wild *H. annuus* in the 1990s also appeared to carry *Pl6*, for example ecotype MPHE-519 from Arizona More recently, further crosses have been made with a wide range of ecotypes and tests were made with race 710 and then race 304 to search for useful *Pl* genes. The results of these tests are presented in Table 2. Thirty two progenies out of 129 showed some resistance to race 710. Nine of the 22 origins with some resistance and sufficient seed for further tests showed susceptibility to race 304. The ecotypes concerned came from different parts of the US: California, Arizona, Nebraska, New Mexico and Texas. It was concluded that they probably carried *Pl6*, so it seems that this gene is very widespread in wild *H. annuus* populations.

(ii) Not *Pl6*: At Montpellier, 2 lines developed from wild *H. annuus* ecotypes MPHE-361 (from Wyoming) and MPHE-829 (from Iowa) have been shown to be resistant to all races tested. Their resistance segregates independently of the *Pl6*, *Pl5/8* and *Plarg* clusters (Table 1). These genes are being mapped and the lines are available to breeders. J. Miller developed HA458, also resistant to all known races from a cross with a *H. annuus* ecotype from Idaho. The resistance gene appears independent of all known clusters (Table 1), and is also being mapped. It is not yet known whether these 3 sources carry the same or different genes, but they certainly appear different from *Pl6.*

Among the crosses made more recently at Montpellier and continued in research since resistant to both races 710 ands 304, there are origins from 13 ecotypes, from: Texas, Wyoming, Oklahoma, Utah, Kansas, Colorado and California (Table 2). It may be some time before the resistance genes they contain are identified as many show considerable self-sterility and require further crosses to cultivated sunflower to obtain sufficient seed by selfing to be able to demonstrate homozygous resistance and so be able to make test crosses and prepare material for mapping. Among these origins, it would be interesting, and quite logical, to find a "*Pl6+",* which has the whole *Pl6* cluster in resistant form, combining the resistances of *Pl1, Pl2* and *Pl6*. Or there is something not known about the structure of this cluster which would make such a form non-viable.

Table 1. Origins of sunflower downy mildew resistance genes and results of test crosses to determine whether they segregate independently

Source line/pool	Origin	Resistance to main French races	gene	Test cross segregations* or publication				
				HA335	XRQ	RHA419	QHP1	PMI3
Resistance from cultivated sunflower								
AD66	953-102-1-1	100	*Pl1*	Vrânceanu and Stoenescu, 1970				
RHA265/266	953-102-1-1	100	*Pl1*					
HA60	953-102-1-1	100	*Pl1*					
RHA274	953-102-1-1	100,304,334	*Pl2*	Zimmer and Kinman, 1972				
HA61	953-88	100,304,334	*Pl2*					
Guyacan/HAR5	953-102-1-1	100,304,314, 334,710,714	Pl_{QHP1}					
QHP1	HAR5 x PRS7*(Pl1*)	100,304,314, 334,710,714	Pl_{QHP1}	70/310	79/348	83/329	--	70/270
Charata/HAR4/ Caburé	(Russian pool x wilds)	100,304,314, 334,710,714	Pl_{QHP1}					
Resistance directly from wild *H. annuus* (*Pl6*)								
HA335/336	HA89x*H.ann*. 423/432 (Texas)	100,703,710	*Pl6*	Miller and Gulya, 1991; Roeckel-Drevet et al., 1996				
HA458	HA434x*H.ann.* (Texas)	100,703,710	*Pl6*	0/292	78/254			
"TP5"	HA434x*H.ann.* (California)	100,703,710	*Pl6*	0/430	98/376			
"MPHE-519"	MPHE-519 x 90R19	100,703,710	*Pl6*	0/153	13/98			
not *Pl6*								
HA458	HA434x*H.ann.* (Idaho)	100,304,314, 334,703,704, 710,714	*Pl?*	133/523	74/223	22/82	16/94	
MPHE-361	90R19x*H.ann.* (Wyoming)	100,304,314, 334,703,704, 710,714	*Pl?*	76/348	87/330	48/267	36/167	52/275
MPHE-829	RT1B11x*H.ann.* (Iowa)	100,304,314, 334,703,704, 710,714	*Pl?*	42/198	69/181	51/200	50/217	73/259
Resistance from *H. argophyllus*								
RHA340	HA89x *H.arg*415	100,304,314, 334,703,704, 710,714	*Pl8*	Miller and Gulya, 1991; Vear et al., 2000				
RHA419	RHA373x *H.arg*1575	100,304,314, 334,703,704, 710,714	Pl_{arg}	Miller et al., 2002; Vear et al., 2003				
"79ARGMTP"	MPHE-92 x FS20	100,304,314, 334,703,704, 710,714	Pl_{arg}	83/391	50/304	0/260	59/257	80/373
PAA1/OQP7	PBP1xAR22	100,304,314, 334,703,704, 710,714	Pl_{arg}	--	34/109	0/106		
Resistance from *H. tuberosus*								
Progress/DM3/ Rf5566		100,304,314, 703,710,704, 714	*Pl5*	Vrânceanu et al., 1981; Miller and Gulya, 1987				
XRQ	HA89xProgress	100,304,314, 703,710,704, 714	*Pl5*	Bert et al., 2001; Vear et al., 2000				
Novinka/XPQ		100,304,314, 703,710,704, 714	*Pl5?*	Vear et al., 1998				
DM2/PMI3	Novinka	100,304,703, 704	P_{PMI3}	Vear et al., 1998				
HIR34	Armair9343xH.tubD19-6	100,304,314	*Pl4*	Leclercq et al., 1970; Vear et al., 1998				

*numbers of susceptible plants in resistance tests with race 710 (703 with PMI3) on test cross progenies (susceptible x (known resistance cluster x new source)F1

Table 2. Downy mildew resistance of *H. annuus* introgressions, susceptible or resistant to race 304

Pl6 ?				Not *Pl6*			
Genotype	Origin	Resistance		Genotype	Origin	Resistance	
	Wild *H. annuus*	710	304		Wild *H. annuus*	710	304
HAS9	Arizona	Seg	**S**	HAS1	Texas	**R**	seg
HAS20	California	Seg	**S**	HAS6	Wyoming	**R**	**R**
HAS46	Arizona	Seg	**S**	HAS40	Texas	**R**	seg
HAS101	Kansas	Seg	**S**	HAS42	Oklahoma	seg	seg
HAS147	California	Seg	**S**	HAS32	Texas	seg	seg
HAS164	New Mexico	Seg	**S**	HAS54	Oklahoma	seg	seg
HAS186	Texas	Seg	**S**	HAS62	Utah	seg	seg
HAS210	Wyoming	Seg	**S**	HAS85	Wyoming	seg	seg
HAS238	Nebraska	Seg	**S**	HAS94	Wyoming	seg	seg
				HAS103	Kansas	seg	seg
				HAS122	Colorado	seg	seg
				HAS156	California	seg	seg
				HAS171	Texas	seg	seg

Resistance from H. argophyllus: RHA340 was developed by Miller and Gulya from a cross between *H. argophyllus* 415 and HA89. The gene was identified as *Pl8*, resistant to all known races, but with pronounced sporulation on cotyledons, in seedling tests although perfectly efficient in the field. Miller et al. (2002) developed RHA419 from RHA373 x H. *argophyllus* 1575 and its gene was mapped by Dussle et al. (2004) to a different LG from *Pl6* and *Pl8*. At INRA, Montpellier a resistant line, 79ARG was developed from an interspecific pool obtained from crossing *H. argophyllus* (MPHE-92) with cultivated sunflower. This line is also resistant to all known races, showing no segregation with the resistance of RHA419. It was also found to have the same marker linkages (ORS610 and ORS543). In studies of quantitative resistance, it was found that some INRA inbred lines (PAA1, OQP7, OQP8) developed from a cross with *H. argophyllus* made by Leclercq in about 1975, and considered to be susceptible to downy mildew when the presence of the slightest spore was considered to show susceptibility, are resistant to race 710 and also to all the other French races. A test cross with RHA419 showed no segregation (Table 1), so it was concluded that this origin also contains *Plarg*.

Resistance from H. tuberosus: Pl5 was first reported by Vrânceanu et al. (1981) and resistant lines were also developed by Miller and Gulya (1987) from the Russian open pollinated variety Progress, obtained at Krasnodar apparently from an interspecific cross with *H. tuberosus*. This resistance was selected to obtain resistance to race 710 (race 4). Other lines, such as the INRA line XRQ, were developed independently in France, from a sample of Progress provided to Leclercq by Novi-Sad. This source has been widely used since *Pl5* gives resistance to all French races except 334, (which is only observed very rarely). Like *Pl8*, it gives type II resistance (sporulation on cotyledons). Incomplete forms of *Pl5* occur: whereas XRQ is resistant to a Spanish isolate of race 330, the differential D5, PM17 is susceptible. The open pollinated variety Novinka, apparently from the same origin as Progress gave the INRA line XPQ, with resistance not distinguishable from XRQ, but from this variety were also derived USDA pool DM2 and the INRA line PMI3, which is resistant to race 703 but susceptible to 710. It seemed likely that its gene was an incomplete *Pl5*, but genetical analyses with races 703 and 304, to which it is resistant, showed segregation in test crosses with XRQ. Using bulk segregant analysis, it showed no linkage with markers in the region of *Pl5/Pl8* or with the Pl6 cluster. The gene Pl_{PMI3} has still not been mapped.

The other resistance source obtained from *H. tuberosus* was HIR34, with a gene denoted *Pl4*. It has a similar range of resistance to *Pl2*, except that it is susceptible to races 334, 307 and a US isolate of race 330, it has type II resistance and does not map in the *Pl2/Pl6* cluster.

Resistance from other species: HA337, HA338 and HA339 were all developed from *H. praecox* by Miller and Gulya (1991), with a gene designated *Pl7*, but which has not been distinguished from *Pl6* by its resistance to different races or its map position. At the same time as the interspecific pool from *H. argophyllus* was studied, a number of other interspecific pools developed at INRA Montpellier were also tested for their resistance to race 710. All showed some downy mildew resistance. Progenies apparently homozygous for resistance to 710 were obtained from a *H. neglectus* pool but these were susceptible to

races 304, 714 and 334, suggesting that a *Pl6* type gene was present. Interspecific pools from *H. petiolaris fallax, H. resinosus* and *H. debilis*, showed some resistance to 710 but no homozygous lines were obtained. For a pool from *H. occidentalis*, it was concluded more recently (Vear, 2006) that resistance may be under quantitative control rather than *Pl* genes.

In more recent studies, resistance to both races 710 and 304 has been fixed in introgression lines from *H. resinosus, H. strumosus, H. debilis* and *H. tomentosus*. These lines are in the course of study to determine whether they provide new *Pl* genes.

DISCUSSION

Resistance genes all appear to come from quite recent crosses with wild *Helianthus*, and in particular wild *H. annuus*. What is identified depends on the resistance requirement. New sources of *Pl1* and *Pl2* probably exist quite widely but are of little interest in modern breeding and so are not introgressed. In contrast, tests made with races 710 or 730 have shown that *Pl6* is present in many wild *H. annuus* ecotypes, most frequently in southern US but from Texas to California. In addition, the gene *Pl7*, from *H. praecox* and the resistance in a pool from *H. exilis* also appear to be the same. There does appear to be at least a second cluster from wild *H. annuus*, but the results of mapping of resistance derived from MPHE-361, MPHE-829 and HA458 are necessary to conclude whether their resistance genes are indistinguishable. The absence of segregation between *Pl5* (from *H. tuberosus*) and *Pl8* (*H. argophyllus*) was surprising, it was questioned whether these genes, which appear to have the same structure, were the result of natural interspecific crosses, or whether, in the multiple interspecific hybridisation at Krasnodar, the open pollinated variety Progress included a gene from *H. argophyllus*. However, since then, Pl_{arg} has been identified from three completely independent crosses at Fargo, Montpellier and Clermont-Ferrand, over 20 years and with quite different *H. argophyllus* ecotypes. Now it seems that *H. argophyllus* has only one "*Pl* gene" (it may be that new races will show some differences between them). So what is the relation between *Pl8* and Pl_{arg}? It could be that *H. argophyllus* contains the same genes as *H. tubersosus* or that there are sites in the sunflower genome (susceptible alleles) where these resistance genes become integrated so that the cultivated genotype used in the interspecific cross may determine the position of interspecific *Pl* genes.

At present, wild *H. annuus* appears the most fruitful source of *Pl* genes, but *Pl6* is often found, and it is this species with which it has been easiest to work. It is also true that the sources derived from both *H. annuus* and *H. tuberosus* show variation in the numbers of downy mildew races controlled, giving the appearance of more "new" genes than there really are. *Pl1* appears to be a *Pl2-,* having lost resistance to races such as 304*,* and forms of *Pl6* which had lost resistance to races 100 and 300 were obtained experimentally (Vear et al., 1997). For *Pl5*, there appear to be several sources differing slightly in the races they resist, although no within-cluster recombination has been obtained intentionally. It is also true that, with sporulation on cotyledons, individual plants or single progenies with incomplete forms of *Pl5* and *Pl8* may be difficult to identify. In contrast, so far, there do not appear to be any *Plarg-*. This last resistance may be a different structure from the other clusters, but its appearance from 3 different crosses suggests that *H. argophyllus* is not very rich in different *Pl* genes.

In the last 20 years breeders have spent a lot of effort on introducing new *Pl* genes into their best lines following changes in *P. halstedii* races. Since 2003 studies have been made on quantitative, hopefully non-race specific, resistance with levels that could be sufficient alone but which certainly would be of use in combination with *Pl* genes (Tourvieille de Labrouhe et al., 2008). QTL have been identified (Vear et al., 2008) which appear independent of the known *Pl* gene clusters, but it is important to continue identification and mapping of the other sources of complete resistance to check that quantitative resistance is not controlled by incomplete major genes. Overall, if it is found that, among the new sources of complete resistance, there are some new *Pl* genes and that quantitative resistances are different and not race specific, breeders should have the resources necessary to provide durable resistance to downy mildew quite rapidly. In addition, in the long term, if it becomes possible to introgress genes from the perennial *Helianthus* species, the small successes so far from *H. tubersosus* and the apparent resistance in *H. resinosus, H. tomentosus and H. occidentalis*, suggest that new and perhaps different types of downy mildew resistance could become available.

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