DE GRUYTER HELIA 2015; 38(63): 149–162

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Recent Changes in the Pathogenic Variability of *Plasmopara Halstedii* (Sunflower Downy Mildew) Populations from Different Continents

DOI 10.1515/helia-2015-0009
Received June 8, 2015; accepted July 10, 2015; previously published online August 12, 2015

Abstract: The obligate biotrophic Oomycete, *Plasmopara halstedii*, causal agent of sunflower downy mildew, is capable of producing new pathogenic races over time. Although changes in the *P. halstedii* race composition were reviewed for the first time in 2007, since then the pathogen has continued to change its virulence character dramatically. There was a need, therefore, to update information on pathogenic diversity of *P. halstedii* by making accounts of the temporal and spacial changes in the pathogen populations in North and South America and Europe. This paper, based on current publications and personal communications, attempts to present an accurate overview of races in Europe and Americas for the last 7 years.

Keywords: pathogenic race, *Plasmopara halstedii*, temporal and spacial change

Introduction

Sunflower downy mildew, incited by the biotrophic Oomycete *Plasmopara halstedii* (Berlese et de Toni), has long been considered one of the most devastating sunflower diseases worldwide. The incidence and distribution of the disease is due to its high genetic variability, particularly in terms of the production of pathogenic races or pathotypes. Prior to 1980, only two races of *P. halstedii* were known, one each in Europe and North America (Zimmer, 1974). Since 1980, however an ever increasing number of races have been identified, aided by pathologists around the world studying this pathogen. The use of many resistance genes has also induced changes in the race diversity of this pathogen.

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The dramatic changes in *P. halstedii* race composition were reviewed for the first time in 2007, covering race composition in North and South America and Europe (Gulya, 2007). Since then the pathogen has continued to change its virulence character significantly, most probably due to the use of new resistance genes in sunflower hybrids. Therefore, there was a need to update the information on *P. halstedii* races and their changes from different parts of the world.

In this review article, an attempt has been made to document temporal and spacial alterations that have occurred in a number of countries since 2007, as compared to the previous years. Our presentation is based on information received both from the literature and from personal communications with sunflower pathologists from different countries in Europe, North and South America.

Overview of *Plasmopara halstedii* races in 2007–2013

Based on a number of relevant journal articles, conference presentations and reports, as well as personal communications with sunflower pathologists from many of the sunflower producing countries, at least 24 *P. halstedii* races in Europe (Table 1) and 40 races in the Americas (Table 2) were identified within the last 7 years. In comparison, only 13 races were recorded in Europe and 20 in the Americas as of 2007 (Gulya, 2007), also depicted in Tables 1 and 2. These tables allow us to demonstrate the dynamics of *P. halstedii* population changes in the different countries over time. A total of 14 countries are surveyed in this paper and, of these, there are only three (Argentina, Russia and Spain) where the race composition has shown little or no change between the two time periods, i.e. until and after 2007. In most of the other countries some races have disappeared, and/or new ones arisen between these two surveyed periods. One should mention, however, that there are no data available from the Czech Republic before, or from Turkey following 2007 (Table 1).

The highest pathogenic diversity of *P. halstedii* recorded among the countries involved in this paper exists in Canada, the USA and in France, with 18, 21 and 13 documented races, respectively, for the period of 2007–2013.

In Canada, based on accurate and long-lasting field surveys carried out in recent years, Rashid (2014) reported a detailed race composition for the period 2007–2013 and he emphasized that out of the 18 existing races, 320, 700, 720, 730 and 732 were the predominant ones. It is also interesting that at least three of the races (120, 321, 331) identified in Canada are considered as unique and not have been recorded in any other country (Rashid, 2014).

Table 1: *Plasmopara halstedii* race distribution in Europe before and after 2007.

Vir. Code	BG	CZ	F	D	H	I	RO	RUS	SRB	E	TR
100	X		X	X,Y	X,Y	X	X,Y	X,Y	X,Y	X,Y	
300	X,Y		X	X,Y	X	X	X,Y	X,Y		X,Y	X
304			X,Y								
307			X,Y								
310				X,Y			Y	X,Y		X,Y	
314			X,Y								
320				Y							
330	X,Y			X,Y	X,Y		X,Y	X,Y		X,Y	X
334			X,Y								
700	X,Y	Y	X		X,Y	X,Y	X,Y	X,Y	X,Y	X,Y	X
703			X,Y			X,Y				X,Y	X
704		Y	X,Y		Y	Y					
707			X,Y								
710		Y	X,Y	X,Y	X,Y		Y	X,Y		X,Y	X
713											X
714		Y	X,Y		Y						
717			X,Y								
721	Y										
730		Y	X,Y	X,Y	X,Y		X,Y	X,Y	X,Y	X,Y	X
731	Y										
750				Y							
770		Y	Y	X,Y						Y	X
773											X
774			Y								
Total	4 + 5	0 + 6	14 + 13	7 + 9	6 + 7	4 + 3	5 + 7	7 + 7	3 + 3	8 + 9	9 + 0

Notes: Explanation: X means before 2007, Y means after 2007.
BG = Bulgaria, CZ = Czech Republic, *F* = France, *D* = Germany, *H* = Hungary, *I* = Italy, RO = Romania, RU = Russia, SRB = Serbia, *E* = Spain, TR = Turkey.

In Argentina, the race diversity of *P. halstedii* has remained stable during the last two decades so that no changes have been detected and not any of these races (300, 330, 710, 730, and 770) were reported as being predominant (Bertero de Romano *et al.*, 2010). There was no indication of any of the five races, 300, 330, 710, 730, and 770 being as predominant among them.

In the United States the number and proportion of *P. halstedii* races isolated from sunflower had been quite stable during the first decade of the twenty-first century. From the year 2000 through 2008, a total of 11 races were identified from 350 samples collected from the states comprising the major production area of the northern Great Plains (North Dakota, South Dakota, Minnesota) and the central or High Great Plains (Nebraska, Colorado and Kansas) (Gulya, 2008).

Table 2: *Plasmopara halstedii* races in Americas before and after 2007.

Vir. Code	Argentina	Canada	USA
100		Y	X,Y
120		Y	
300	X,Y	X,Y	X,Y
310		X	
314			Y
320		Y	
321		Y	
323		X	
330	X,Y		X
331		Y	
333		X	
334		Y	Y
500			
502			
560			
563			
700		X,Y	X,Y
702		X,Y	
703		X,Y	X
704			Y
710	X,Y	X	X,Y
713			Y
714			Y
720		Y	
722		X,Y	
723		X,Y	
730	X,Y	X,Y	X,Y
731		X	
732		X,Y	X,Y
733		X,Y	X,Y
734			Y
735			Y
737			Y
740			X,Y
743		X	
754			Y
770	X,Y	X,Y	X,Y
772		X,Y	X,Y
773			Y
774			Y
Total	5 + 5	17 + 18	12 + 21

Note: Explanation: X means before and Y means after 2007.

Of the 11 races found, races 730 and 770 were dominant, comprising 66%. This is very similar to the situation observed in Europe where races 710, 730 and 770 were the dominant virulence phenotypes.

In contrast to the situation in France, where the first race to overcome the Pl-6 gene designated as 304 was found in 2000, it was not until 2009 in the USA that a race capable of overcoming the Pl-6 was found. In that year, outbreaks of downy mildew were noted in fields planted to supposedly downy mildew-resistant hybrids, which prompted a concentrated survey to examine fields in north-central North Dakota, near the Canadian border. From a total of 49 fields, two new “virulent” races (capable of overcoming the Pl-6 gene) were found in 24% of the samples. These first two virulent races were 714 and 734 (Gulya and McMullen, 2011; Gulya, 2012). The discovery of races overcoming the Pl-6 gene, widely used in hybrids labeled as DMR (downy mildew resistant) prompted a renewed effort to annually collect *P. halstedii* samples, and to do so in an orderly, unbiased manner. Personnel of the USDA-ARS Sunflower Unit, extension personnel from state universities in North Dakota, South Dakota, and Nebraska, plus researchers from private seed companies and chemical companies all assisted in the collection of *P. halstedii* samples.

In the 5 year period from 2009, when the first “Pl-6_ virulent” races were identified, through 2013, a total of 520 *Plasmopara* samples were collected and characterized by USDA personnel in the Fargo, ND laboratory (Gulya *et al.*, 2013). Downy mildew incidence varied greatly from year to year, due to environmental conditions, and annual sampling numbers thus varied from a low of 39 to a high of 160. Three new races were identified in 2010, and another four new races were found in 2011, while no new additional Pl-6 virulent races were identified in 2012–2014. The nine Pl-6 virulent races identified in the U.S. during the 2009–2014 periods were 314, 334, 704, 714, 734, 735, 737, 754 and 774. Races 734 and 774 each comprised one-third of the Pl-6 virulent isolates, and, combined with race 714, these three races comprised 93% of the “virulent” races. The total of Pl-6 virulent races comprised 38% of the 520 isolates studied. The Pl-6 virulent races were found primarily in North Dakota, the state with historically the highest sunflower production area, but Pl-6 virulent races were also recovered from South Dakota, Minnesota and Nebraska, indicating that their distribution is likely region wide (Gulya *et al.*, 2014).

When the U.S. *P. halstedii* population developed resistance to the widely used seed treatment mefenoxam in the late 1990s, most U.S. seed companies began an earnest effort to use USDA-released Pl-genes to produce hybrids with resistance to “all known races.” In 1988, a series of USDA lines were released which had three new Pl-genes, derived from wild *Helianthus* (specifically *H. annuus, H. praecox* and *H. argophyllus*). The Pl-6 gene, found in HA-335 and HA-336, and the Pl-7 gene, found in HA-337, HA-338 and HA-339, were the most widely used, while the Pl-8 gene, found in RHA-340, was less utilized as it sometimes displayed "cotyledon-limited sporulation" which made resistance evaluations confusing at times. In tests with the nine "virulent" new races, most commercial hybrids labeled as "DMR" were completely susceptible. A very few "DMR" commercial hybrids were found to be resistant to all new races, and these hybrids contained the Pl-15 gene, developed by NIDERA in Argentina (Bertero de Romano *et al.*, 2010). The USDA lines which continue to be resistant to the new races include RHA-340 (Pl-8 gene), HA-419 and HA-420 (Pl-arg), HA-458 (Pl-17) and TX-16R (unknown Pl gene), as well as the Pl-15 gene developed in Argentina. The USDA has released several inbreds with new Pl-genes, such as Pl-17, and have identified more resistance in wild *Helianthus*. Thus there will be newer sources of *P. halstedii*-resistance available to public breeders globally.

In France a large number of pathogenic races have been identified, suggesting that the pathogen population has evolved rapidly resulting in much more diversity in virulence compared with that in other European countries. Tourvieille and other sunflower pathologists were able to identify 14 races before 2007, and since then two more virulent races were identified and three others not detected, giving a total number of 13 races at present (Tourvieille *et al.*, 2012; Gascuel *et al.*, 2014). This diversity may be explained in part by the fact that in France widespread and detailed surveys have been made each year by the Ministry of Agriculture and technical advisory organisations to provide rapid detection of new races. Observations were made not only when there was a high incidence of downy mildew but also when there were symptoms on only a few plants of hybrids defined as resistant to known downy mildew races. Since 1990, on average, about 50 isolates of *P. halstedii* have been characterised each year, providing a good idea of the diversity of this pathogen present in France (Moinard, 2015).

These surveys not only permitted identification of new pathotypes (770 and 774) since 2007, but also showed that three other pathotypes (100, 300 and 700) have not been isolated in France in the last 10 years. Furthermore, not all identified pathotypes have the same economic impact, which depends on their virulence (pathogenic fitness), the sources of genetic resistance in current hybrids and also on pathogen resistance to available fungicides. For example, race 714 is frequently resistant to mefenoxam, the only approved seed treatment in France. In 2006 pathotypes 703 and 710 were dominant (53% and 40% of samples, respectively). In contrast, in 2014 pathotype 714 was predominant (82% of isolates collected).

Surveys over the entire country (~1,000 fields/year) with characterisation of pathotypes, especially with samples collected from presumably resistant hybrids, have made it possible to estimate the rate of spread of virulent pathotypes. In France, all the regions where sunflower is grown were contaminated by race 710 in less than 15 years (Figure 1) in spite of obligatory control regulations (seed treatment and rotations).

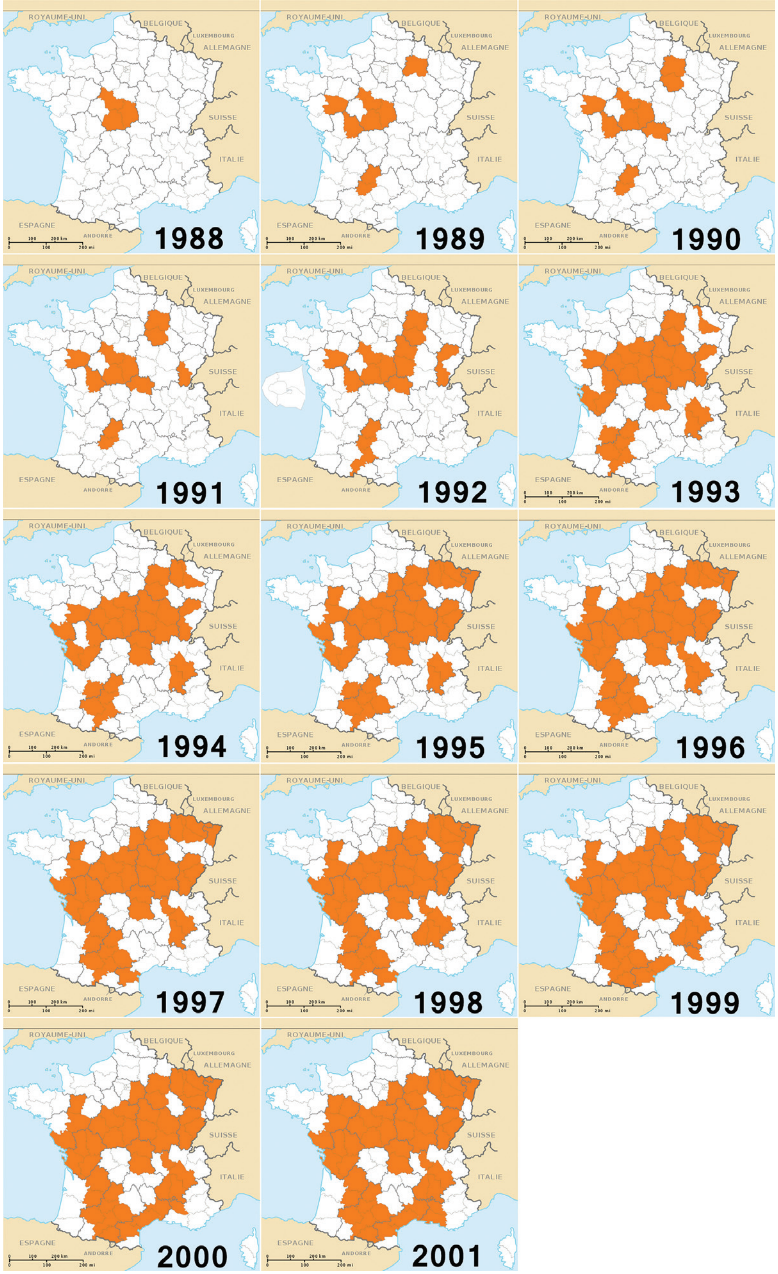

Figure 1: Spread of *Plasmopara halstedii* race 710 in France between 1988 and 2001 (Suffert, 2014).

Similarly, pathotype 714, which first appeared in 2002, was found in four out of the 16 departments by 2014. Its high level of virulence, aggressiveness and resistance to fungicide treatments means that it could cause problems in future years.

As for other European countries, both Germany and Spain are leading at present in term of the number of races existing in these two countries. Thus, in Germany, Spring and his research group have been studying the genetic structure of local *P. halstedii* populations. Based on regular field surveys in the recent years, the race composition in Germany has changed to some extent as compared to the pre-2007 period. Except for the prevalent races 310, 330, 710 and 730 (Rozynek and Spring, 2000), new races 320 and 750 have been identified (Spring, personal communication). Thus, no races capable of overcoming the Pl-6 gene have been found to date in Germany.

In Spain, the situation is different from that of Germany since the race composition has remained almost stable, except for a new race 770, identified recently (Schlatter, 2012). However, the relative dominance of some of the eight races and their geographical distribution has varied over time. While race 310 appeared to be the most frequent one in southern Spain (at 86%), races 100, 330 or 730 dominated outside this area (Molinero-Ruiz et al., 2008). Furthermore, races 300 and 700, initially found in 2000, were absent from subsequent surveys for over a decade, having only been recently found during 2013/2014 surveys (Molinero-Ruiz, personal communication).

In Russia the *P. halstedii* race situation is described in details in the recent publications of Antonova *et al.* (2008) and Guchetl *et al.* (2012). Of the seven races identified in the northern Caucasus districts of Adygea Republic, Krasnodar and Rostov areas, there are three races (330, 710 and 730) which dominate and the race composition appears to remain stable with no new race identified during recent years. In Bulgaria, there are five races, 300, 330, 700, 721 and 731 identified by Shindrova (2010). Of these, race 700 has the largest area of occurrence (in northern Bulgaria) and comprises 46% of the downy mildew population. It is interesting to note that race 100, previously common in the country, has not been recorded recently. This can be explained by the widespread use of Pl-genes conferring resistance to race 100.

In Romania, Pacureanu *et al.* (2010) reported the appearance of two new races, 310 and 710, along with the older ones 100, 300, 330, 700 and 730. Of these, 100 and 300 were considered to be predominant. Thus, in Romania the least virulent race (100) is still found, and this might be explained if old open-pollinated cultivars, lacking any Pl-genes, are still cultivated.

In Hungary, up to recent years, no changes have occurred in the *P. halstedii* populations with regard to their virulence structure, except that race 300 seems to have disappeared (Virányi, 2008). This situation, however, changed dramatically in 2010 and subsequent years. First, Rudolf *et al.* (2011) reported that a new race, 704, was found in a relatively small area in the south-eastern part of Hungary in 2010. This race spread widely the following year. Meanwhile, another new race, 714 was detected in 2013 in the eastern part of the country (Bán *et al.*, 2014a,b). With these two races, the Hungarian pathogen population consists of seven races at present. Even with the appearance of new races, the same races, 700 and 730, continue to be predominant in Hungary (Virányi, unpublished). However, there are no data available to date of the actual portion of these races within the Hungarian *P. halstedii* population.

In Serbia, all races collected prior to 2007 were 100, 700 and 730 (Masirevic, 1998) and of these, 730 remained predominant to date. As of the post 2007 period, it might be possible that the local *P. halstedii* populations could follow a somewhat similar change in race evolution to the neighbouring countries such as Bulgaria, Romania and in particular Hungary. However, the documentation of any change in the pathogen population requires an extensive sampling in space and time. To our best knowledge Serbian scientists have been involved in this work so that new records are foreseen from this country as well.

In the Czech Republic, Trojanova *et al.* (2013) has recently published a short note of the pathogenic races in this country. According to their report, races 700, 704, 710, 714, 730 and 770 have been identified during the 2007–2013 years from different parts of the country.

Finally, Italy appears to be a country with much less pathogenic variability so far. Two races, 700 and 703 have been identified prior to 2007 (Tosi and Zazzerini, 2004), and the appearance of a third one, race 704, was reported by Tosi and Beccari (2007). No more records are available from this country and it is not known if annual surveys are made or their extent.

Discussion and conclusions

As mentioned previously, this review has made an attempt to show the temporal and spacial changes in the pathogenic diversity of *P. halstedii* for the years 2007 to 2013, in a comparison to previous decades (Gulya, 2007). Based on information from refereed publications, and from personnel communications from sunflower pathologists in different countries, it can be concluded that *P. halstedii* has not only preserved but also improved its ability to evolve genetically. As a result, many new virulent phenotypes, commonly called pathogenic races, have appeared within a relatively short period of time (Tables 1 and 2). It is worth mentioning that all country reports on races were based on an internationally accepted identification system having been used by each data supplier. In viewing these data, particularly the differences in race numbers by country, the question arises, what is the reason for this situation. For explanation, one should consider several factors, such as (i) the history of sunflower production and its pathogen in different countries, (ii) the intensity of race identification efforts, and (iii) the efforts of public and private breeders to use specific Pl-resistance genes. For example, in Canada, the United States and France, each with diverse pathogen populations, can equally be characterized as leaders in sunflower production, having a long coexistence of host and pathogen, as well as conducting intensive breeding programmes over many decades (Sackston, 1981; Tourvieille *et al.*, 2005; Gulya, 2007).

From the various country reports it seems likely that, apart from the number of races recorded in a given area, there are just a few races that predominate over Europe. Thus, during the 7-year period between 2007 and 2013, races 330, 700, 710 and 730 were found to be the most prevalent ones in Europe. Of these, race 700 and 730 were reported from 8 countries, while race 710 occurred in seven countries (Table 1). It seems therefore that the occurrence and distribution of races does not necessarily correspond to the geographical localities of a particular country. In other words, no correlation could be detected between the existence of a race in a country and its neighbourhood areas. Furthermore, if we compare the list of dominant races in Europe before 2007 (Gulya, 2007) with that of the following period, with a few exceptions, the two lists are similar to each other, suggesting that despite the appearance of the several new, more virulent races, the sequence of dominant races has remained stable.

Considering the complex of *P. halstedii* virulence diversity in a given country or continent over time, we can speculate how these new races appear. Theoretically, there are two possibilities for this change, either by seed transmission of a „foreign race" or by local evolution of a new virulent race. In the first case, the more intensive, and free seed trade may facilitate race distribution, whereas in the second, the breeding programmes using new resistance genes exert a strong selection pressure on the pathogen. To shed light on these changes, newer molecular techniques to study the mechanism of population polymorphism are becoming important. Recently, researchers in several countries, such as France (Ahmed *et al.*, 2012; Delmotte *et al.*, 2008), Germany (Thines *et al.*, 2005, Spring *et al.*, 2006), Russia (Guchetl *et al.*, 2012), Argentina (Bertero de Romano *et al.*, 2010), and in the United States (Mulpuri *et al.*, 2009; Qi *et al.*, 2015) have become more successful in characterizing the *P. halstedii* genome as regards its genetic virulence factors. Their results may help to understand and potentially forecast the intensity and direction of spread of new pathogen races.

In conclusion, the increasing number of *P. halstedii* races recently identified in many countries shows that this plant pathogen continues to present a significant challenge for effective disease management. In the future, however, when specific markers for virulence become available, it will be necessary to check whether all the races announced do exist in the given area/country. Chemical control is tenuous or short lived due to evolving fungicide tolerance, and governmental registration of new fungicides is a slow process, and different in each country. Thus, the introduction of new hybrids with improved genetic resistance to the pathogen may remain the best possibility for successful, long term disease management. However, because of the ability of *P. halstedii* to rapidly evolve new races, as also shown in this review, traditional use of single, race-specific resistance genes may not insure long-lasting success. Instead, novel approaches are required for future breeding programmes and one of these could be the use of the quantitative resistance. In France, Vear and her research group have recently achieved positive results in finding germplasm with significant quantitative resistance to *P. halstedii* (Vear *et al.*, 2007). Furthermore, their findings suggest that, although the effectiveness of this type of resistance alone was not sufficient, it could be improved to an acceptable level when combined with one or two dominant Pl genes (Tourvieille *et al.*, 2008). Since reliance on one single disease management strategy, whether genetic, chemical, or cultural, is destined to become overcome by pathogens, the wisest strategy for long-term control of *P. halstedii* is a unified, multi-pronged approach, optimistically combining chemicals of different modes of action, multiple resistance genes, and simple, but effective crop rotation.

Acknowledgements: The authors are indebted to pathologists from many countries by providing either refereed publications, unpublished reports or personal communications regarding the identity of *P. halstedii* races in their respective countries. These contributors include: Tatyana Antonova (Russia), Rita Bán (Hungary), Amelia Bertero de Romano (Argentina), Norma Huguet (Argentina), Ales Lebeda (Czech Republic), Stevan Masirevic (Serbia), Leire Molinero-Ruiz (Spain), Maria Pacureanu (Romania), Khalid Rashid (Canada), Pepa Shindrova (Bulgaria) and Otmar Spring (Germany).

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