Dynamics of Race Structures of the Rice Blast Pathogen Population in Heilongjiang Province, China From 2006 Through 2015

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Abstract

Rice blast caused by the fungus *Magnaporthe oryzae* is one of the most destructive diseases of rice. Its control through the deployment of host resistance genes would be facilitated by understanding the pathogen's race structure. Here, dynamics of race structures in this decade in Heilongjiang province were characterized by Chinese differential cultivars. Two patterns of dynamics of the race structures emerged: both race diversity and population-specific races increased gradually between 2006 and 2011, but they increased much more sharply between 2011 and 2015, with concomitant falls in both the population-common races and dominant races. Four races (ZD1, ZD3, ZD5, and ZE1) were among the top three dominant races over the whole period, indicating that the core of

the race structure remained stable through this decade. On the host side, the composition of resistance in the cultivar differential set could be divided in two: the three *indica*-type entries of the differential set expressed a higher level of resistance to the population of *M. oryzae* isolates tested than did the four *japonica*-type entries. The cultivars Tetep and Zhenlong 13 as well as two additional resistance genes α and ε were confirmed as the most promising donors of blast resistance for the local rice improvement programs.

Keywords: cereals and grains, disease development and spread, disease management, epidemiology, field crops

Pathogen races (also referred to as physiological races or pathotypes) are defined by their interaction with a set of host cultivars that each carry a distinct profile of known major resistance genes (Atkins et al. 1967; Feng et al. 2018; Kolmer and Hughes 2018; Liu et al. 2017; Wang et al. 2017). Although a number of studies have addressed the race structure of certain plant pathogens, little attention has been paid to simultaneously characterizing both temporal and spatial dynamics of race structures (Chen et al. 2001; Dorrance et al. 2016; Kawasaki-Tanaka et al. 2016; Kolmer and Hughes 2018; Liu et al. 2017; Wang et al. 2017; Yang et al. 2004; Zhang et al. 2017). Host resistance is often conditioned by a single gene. It tends to follow the gene-for-gene model so that, when the resistance gene no longer recognizes a pathogen's avirulence gene owing to a change in that gene, the result is an abrupt loss in resistance, and disease ensues (Flor 1971; Wu et al. 2014; Zhang et al. 2015). Concomitantly, the deployment of new host resistance genes drives

alterations in a pathogen's race structure (Mekwatanakarn et al. 2000; Wang et al. 2017; Wu et al. 2014; Zhang et al. 2015, 2017). Characterizing and monitoring the dynamics of pathogen population race structures can contribute to devising a sustainable strategy to control plant disease through the deployment of appropriate resistance genes (Hu et al. 2002; Kawasaki-Tanaka et al. 2016; Kolmer and Hughes 2018; Liu et al. 2017; Wang et al. 2017; Zhang et al. 2017).

The largest rice production area in China is in the northeastern province of Heilongjiang (HLJ). The area planted locally to rice increased from 1.99 million hectares (Mha; 6.9% of the national rice production area) in 2006 to 4.01 Mha (13.3%) in 2015; in terms of production, grain harvest has risen from 13.6 million tons (Mt; 7.5% of the national total) to 22.0 Mt (10.6%) (Zhang 2018). Rice blast caused by the heterothallic ascomycete *Magnaporthe oryzae* represents one of the most serious biotic constraints on yield in rice (Wang et al. 2017; Zhang et al. 2017; Zhao et al. 2018). Although a previous study compared the race structure of the HLJ *M. oryzae* population with that present in other parts of China (Zhang et al. 2017), the focus of this investigation was the characterization of the dynamic behavior of the HLJ *M. oryzae* population over the previous decade. To this end, the interaction between *M. oryzae* isolates sampled at various time points during the period 2006 through 2015 and a set of Chinese differential cultivars (CDCs) was tested. At the same time, the *M. oryzae* resistance genes present in the differential set of cultivars was defined, thereby providing direct information to rice breeders regarding the resistance genes being used in the rice breeding programs during the period.

Materials and Methods

Pathogen isolate and inoculum preparation. Diseased rice panicles were sampled from fields across HLJ from 2006 to 2015. Standard methods (Zhang 2018; Zhang et al. 2017) were used to both derive and store single-spore isolates of *M. oryzae* from these samples. The race structures of the three populations Pop-06, Pop-11, and Pop-15 were subjected to investigation of race structure dynamics over a decade. Pop-06 consisted of 97 isolates that were recovered from 269 panicle samples collected from 10 counties; Pop-11

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contained 103 isolates recovered from 219 samples collected from 11 counties, and Pop-15 contained 96 isolates recovered from 317 samples collected in 19 counties (Supplementary Table S1) (Zhang 2018).

Inoculation with *M. oryzae* and scoring for disease. Inoculum of each isolate was prepared as described in Pan et al. (1996) and modified by Zhang (2018) and Zhang et al. (2017). The concentration of the inoculum suspension was adjusted to 10 to 50×10^4 conidia per milliliter for inoculation. The CDC set, which comprised three *indica*-type entries (cultivars Tetep, Zhenong 13, and Sifeng 43) along with four *japonica*-type entries (cultivars Dongnong 363, Kando 51, Hejiang 18, and Lijiangxintuanheigu [LTH]), was challenged with each of the 296 *M. oryzae* isolates. Each CDC entry was represented by 10 hydroponically raised seedlings following methods described by Zhang (2018). The inoculum was sprayed on seedlings at the four- to five-leaf stage. The host reaction was scored 6 days post-inoculation using the Pan et al. (1996) numerical scale (0 to 2: resistant; 3 to 5: susceptible). Inoculation of each CDC entry with each isolate was carried out at least twice in independent inoculations. In cases of inconsistency, the highest score recorded for the host reaction was used.

Race identification. Each of the seven CDC entries was assigned a race code (All China Corporation of Research on Physiological Races of *Pyricularia oryzae* 1980), which combines both an alphabetical component and a numerical component, namely Tetep, race code A64; Zhenlong 13, race code B32; Sifeng 43, C16; Dongnong 363, D8; Kando 51, E4; Hejiang 18, F2; and LTH, G1 (Supplementary Table S2). A given isolate of *M. oryzae* was initially assigned its race group according to its compatible reaction produced on the alphabetically upper CDC entry (from A to G), after which race number (a numerical value) was assigned, representing the sum of the codes corresponding to the remaining entries on which an incompatible reaction was observed, followed by adding 1 to the numerical value to avoid coding races as A0 and B0. The suffix H was assigned to all isolates that were incompatible with all seven CDC entries (All China Corporation of Research on Physiological Races of *Pyricularia oryzae* 1980; Zhang et al. 2017).

Data analysis. Race structure was dissected into four aspects with nine parameters (Supplementary Table S3). The total race frequency f_{tr} $[(tr/N) \times 100\%]$ and the race diversity index h_{rdi} $[(N/N - 1)(1 - \sum x_i^2)]$ were used to represent race diversity; in the latter case, the index gets closer to one as the population becomes more diverse: the population common race frequency f_{pcr} $[(pcr/tr) \times 100\%]$, the population common race isolate frequency f_{pcri} $[(pcri/N) \times 100\%]$, and the total population common race isolate frequency f_{ipcri} $[(tpcri/N) \times 100\%]$ for common race structure; the population specific race frequency f_{psr} $[(psr/tr) \times 100\%]$ and the population specific race isolate frequency f_{psri} $[(psri/N) \times 100\%]$ for specific race structure; and the top three race isolate frequency f_{t3ri} $[(t3ri/N) \times 100\%]$ and the total top three race isolate frequency f_{tt3ri} $[(tt3ri/N) \times 100\%]$ for dominant race structure. In these expressions, N represented the number of the isolates within a population, tr represented the number of races identified within a given population, x_i represented the frequency of race

$\#i$, pcr represented the number of population-common races across all three populations, $pcri$ represented the number of population-common race isolates within a population, $tpcri$ represented the total number of population-common race isolates within a population, psr represented the number of population-specific races within a population, $psri$ represented the number of population-specific race isolates within a population, $t3ri$ represented the number of top three race isolates within a population, and $tt3ri$ represented the total number of the top three race isolates within a population. To test a hypothesis that the race structure has not changed in this decade in HLJ, a χ^2 test was applied to pairwise comparison for Pop-11 versus Pop-06 and Pop-11 versus Pop-15 for the first and second half of the period, respectively, for the key parameters.

The dynamic behavior of the host resistance gene content was quantified using the parameters cultivar resistance frequency f_{CR} $[(CRI/N) \times 100\%]$ and the total cultivar resistance frequency f_{TCR} $[(TCRI/TN) \times 100\%]$, where CRI represented the number of isolates that were avirulent on a given CDC entry, $TCRI$ represented the total number of isolates that were avirulent across all three populations, and TN represented the total number of isolates of all three populations (Zhang et al. 2017). For clarity, each CDC entry was given an overall resistance rating (high: >85%; intermediate: 60 to 84%; and low: <60%) following Zhang et al. (2017).

Results

Race diversity. Of the three *M. oryzae* populations, Pop-15 was more diverse than either Pop-06 or Pop-11. The 25 races detected in Pop-15 were distributed across seven of the eight groups, featuring an f_{tr} value of 26.0% (Table 1). Within both Pop-06 (12 races detected) and Pop-11 (14 races), six of the eight groups were represented, equivalent to f_{tr} values of 12.4 and 13.6%, respectively. The h_{rdi} values were consistent with those of f_{tr} , namely 0.800 (Pop-06), 0.813 (Pop-11), and 0.947 (Pop-15). Thus, there was an increase in race frequency and diversity during the first half of the decade and an even greater increase in race frequency and diversity during the second half of the decade.

Common race structure. In all, nine races (ZB25, ZB33, ZB57, ZC1, ZC9, ZD1, ZD5, ZE1, and ZF1) were identified as being represented in all three populations, leading to estimated f_{pcr} values of 75.0% in Pop-06, 64.3% in Pop-11, and 36.0% in Pop-15 (Tables 1 and 2). The f_{pcri} values for the set of shared races varied from 32.0 (ZD1 in Pop-06) to 1.0% (ZF1 in Pop-06; ZC1 in Pop-11; and ZB25, ZB33, and ZB57 in Pop-15) (Table 2). The estimated f_{ipcri} values were 93.8% in Pop-06, 90.3% in Pop-11, and 51.0% in Pop-15. The proportions of the common races were greater from Pop-06 to Pop-11 and considerably lower from Pop-11 to Pop-15, indicating

Table 1. Race diversity of three populations of *Magnaporthe oryzae* from Heilongjiang province recovered from symptomatic rice panicles over the period from 2006 to 2015 assessed by challenging a set of Chinese differential cultivars

Parameter	2006 (97) ^a	2011 (103)	2015 (96)
No. of race group	6	6	7
No. of race	12	14	25
Race frequency (f_{tr})	12.4	13.6	26.0
Race diversity index (h_{rdi})	0.800	0.813	0.938
χ^2 for f_{tr} ^b	0.06	3.88 ^c	

^a Numbers shown in parentheses represent the numbers of isolates tested.
^b The χ^2 test was applied to pairwise comparison for Pop-11 versus Pop-06 and Pop-11 versus Pop-15 for the first and second half of the decade, respectively.
^c Significant at the $P = 0.05$ level for a χ^2 .

Table 2. Common races of *Magnaporthe oryzae* in three populations of pathogen recovered from the Heilongjiang region over the period from 2006 to 2015

Race/Parameter	2006 (97) ^a		2011 (103)		2015 (96)	
	No.	f_{pcri}	No.	f_{pcri}	No.	f_{pcri}
ZB25	5	5.2	3	2.9	1	1.0
ZB33	2	2.1	3	2.9	1	1.0
ZB57	2	2.1	2	1.9	1	1.0
ZC1	3	3.1	1	1.0	5	5.2
ZC9	5	5.2	3	2.9	3	3.1
ZD1	31	32.0	28	27.2	12	12.5
ZD5	17	17.5	29	28.2	6	6.3
ZE1	25	25.8	19	18.4	13	13.5
ZF1	1	1.0	5	4.9	7	7.3
f_{pcr}		75.0		64.3		36.0
$\sum f_{ipcri}$	91	93.8	93	90.3	49	51.0
χ^2 for f_{ipcri} ^b		0.07		10.93 ^c		

^a Figures shown in parentheses represent the number of isolates tested.
^b The χ^2 test was applied to pairwise comparison for Pop-11 versus Pop-06 and Pop-11 versus Pop-15 for the first and second half of the decade, respectively.
^c Significant at the $P = 0.001$ level for a χ^2 .

that race structures in both Pop-06 and Pop-11 were stable and changed in Pop-15.

Specific race structure. The numbers of population-specific races in Pop-06, Pop-11, and Pop-15 were one, four, and 13, respectively, resulting in estimated f_{psr} values of 8.3, 28.6, and 52.0%, respectively (Tables 1 and 3). The numbers of isolates were one (Pop-06), seven (Pop-11), and 42 (Pop-15), giving rise to f_{psr} values of 1.0, 6.8, and 42.7%, respectively. Thus, the population-specific races increased steadily from Pop-06 to Pop-15, but population-specific race isolates increased gradually from Pop-06 to Pop-11 and more abruptly from Pop-11 to Pop-15.

Dominant race structure. Three group D races (ZD1, ZD3, and ZD5) and one group E race (ZE1) emerged as the dominant races across the three populations (Table 4). The f_{i3ri} values ranged from 32.0 to 9.4%, whereas the f_{u3ri} values were 75.5% (Pop-06), 73.8% (Pop-11), and 35.4% (Pop-15). ZD1 and ZE1 were the dominant races in all three populations: ZD1 represented 32.0% of Pop-06, 27.2% of Pop-11, and 12.5% of Pop-15; ZE1 was dynamic among the three populations (Table 4). Considering the entire decade, the dominant races were limited to very few races; however, their proportions were slightly reduced from Pop-06 to Pop-11 and greatly reduced from both to Pop-15.

Resistance structure. The resistance gene composition of the CDC entries was based on the conclusions drawn by Zhang et al.

(2017). The level of resistance displayed by the subsets of *indica* and *japonica* types differed markedly when challenged by each of the three *M. oryzae* populations (Table 5). Among the *indica* types, Tetep and Zhenlong 13 expressed a greater level of resistance than other entries, irrespective of which *M. oryzae* population was involved, whereas Sifeng 43 proved to be more resistant when challenged by isolates from Pop-06 than when challenged by isolates from either Pop-11 or Pop-15. All of the *japonica*-type entries performed poorly when challenged with isolates from each of the *M. oryzae* populations; LTH was susceptible to every isolate. Zhenlong 13 was more resistant to *M. oryzae* than Dongnong 363, possibly reflecting the presence of the resistance gene ϵ . The difference between the reactions of Sifeng 43 and Hejiang 18 (especially when challenged by the isolates in Pop-06 and Pop-11) implied that the combination *Pib* + α imparted a superior level of resistance than was provided by *Pia* on its own. Collectively, the resistance composition of the CDC set in this decade reacted differently in terms of resistance between the *indica* and *japonica* subsets to inoculation with the isolates of *M. oryzae*.

Discussion

The race structure of the population of *M. oryzae* in the largest rice cropping area, HLJ, has been repeatedly investigated (Gao et al.

Table 3. Specific races of *Magnaporthe oryzae* in three populations of pathogen recovered from the Heilongjiang region over the period from 2006 to 2015

Population	Specific race (no. of isolates) ^a	Race		Isolate		χ^2 for f_{psr} ^b
		No.	f_{psr}	No.	f_{psr}	
2006 (97)	ZB49 (1)	1	8.3	1	1.0	4.31 ^c 27.06 ^d
2011 (103)	ZA9 (1), ZB37 (2), ZB41 (2), ZC5 (2)	4	28.6	7	6.8	
2015 (96)	ZA21 (1), ZB1 (2), ZB3 (1), ZB5 (3), ZB7 (1), ZB19 (1), ZC3 (3), ZC7 (2), ZC11 (2), ZD3 (9), ZD7 (8), ZE3 (4), ZG1 (5)	13	52.0	42	43.8	

^a Races are ordered according to their alphanumeric code.

^b The χ^2 test was applied to pairwise comparison for Pop-11 versus Pop-06 and Pop-11 versus Pop-15 for the first and second half of the decade, respectively.

^c Significant at the $P = 0.05$ level for a χ^2 .

^d Significant at the $P = 0.001$ level for a χ^2 .

Table 4. Dominant race of *Magnaporthe oryzae* in three populations of pathogen recovered from the Heilongjiang region over the period from 2006 to 2015

Population	Top 3 races and their frequencies						χ^2 for f_{u3ri} ^a
	First (isolates)	f_{i3ri-1}	Second (isolates)	f_{i3ri-2}	Third (isolates)	f_{i3ri-3}	
2006 (97)	ZD1 (31)	32.0	ZE1 (25)	25.8	ZD5 (17)	17.5	0.02 13.50 ^b
2011 (103)	ZD5 (29)	28.2	ZD1 (28)	27.2	ZE1 (19)	18.4	
2015 (96)	ZE1 (13)	13.5	ZD1 (12)	12.5	ZD3 (9)	9.4	

^a The χ^2 test was applied to pairwise comparison for Pop-11 versus Pop-06 and Pop-11 versus Pop-15 for the first and second half of the decade, respectively.

^b Significant at the $P = 0.01$ level for a χ^2 .

Table 5. Resistance genes and resistance frequencies of a set of Chinese differential cultivar entries that were challenged with isolates of *Magnaporthe oryzae* recovered from the Heilongjiang region over the period from 2006 to 2015

Differential cultivar	Race code	Resistance gene	Resistance frequency (f_{CR})			Total resistance frequencies (f_{TCR})
			2006	2011	2015	
Tetep	A64	<i>Pi1</i> , <i>Pi4</i> , <i>Pi54</i>	93.8 ^a	90.3 ^a	95.8 ^a	93.2 ^a
Zhenlong 13	B32	<i>Pik</i> , <i>Pia</i> , β , ϵ	89.7 ^a	96.1 ^a	86.5 ^a	90.9 ^a
Sifeng 43	C16	<i>Pib</i> , <i>Pia</i> , α	89.7 ^a	83.5	74.0	82.4
Dongnong 363	D8	<i>Pik</i> , <i>Pia</i> , β	39.2	36.9	39.6	38.5
Kando 51	E4	<i>Pik</i> , γ	18.6	39.8	36.5	31.8
Hejiang 18	F2	<i>Pii</i> , <i>Pia</i> , δ	0.0	0.0	37.5	12.2
Lijiangxintuanheigu	G1	<i>Pik-l</i>	0.0	0.0	0.0	0.0

^a Higher levels of resistance.

2017; Lei et al. 2011; Li and Zheng 1989; Xin et al. 2016; Zhang et al. 2009), but the influence of season and location on the dynamic behavior of the race structure has not been well defined. In our previous research, the spatial features of the race structure of *M. oryzae* in HLJ were refined on the basis of comparison with other Chinese *M. oryzae* populations (Zhang et al. 2017). In this study, the race structures of three populations of *M. oryzae* recovered from HLJ were temporally characterized by the four aspects with the nine comparable parameters: that is, f_{ir} and h_{rd} for rice diversity (Table 1); f_{pcr} , f_{pcrs} and f_{ipcr} for common race structure (Table 2); f_{psr} and f_{psri} for specific race structure (Table 3); and f_{i3ri} and f_{ti3ri} for dominant race structure (Table 4). This allowed for the recognition of two distinct phases in the development of the population race structure of *M. oryzae* in HLJ: both race diversity and the population-specific races increased gradually between 2006 and 2011, but the increase was much greater between 2011 and 2015, with concomitant decreases in both the number of population-common races and dominant races. Similarly, Liu et al. (2017) provided evidence of an acceleration in the appearance of new races of the wheat stripe rust pathogen in the United States. They detected 171 races of the pathogen between 1968 and 2009, but from 2000 onward, the number of races detected increased at a greater rate than in the previous decades.

The biological basis for the change in population race structure that we detected may reside in the number of rice cultivars cultivated in HLJ over the course of the study period. Whereas 53 cultivars were grown over an extensive area at the beginning of the period of investigation (2006), this number had increased to 92 by 2011, and in 2015, 127 cultivars were planted (Zhang 2018). The time lag observed between the growth of race numbers and the increase in the number of host cultivar probably reflects the time needed for the pathogen to adapt to a more complex spectrum of host resistance genes. Similarly, an analysis of ~1,000 *M. oryzae* isolates collected in United States over the period from 1959 to 2015 suggested that race structure varied more over time than over space, leading to the conclusion that host-driven selection is the major determinant of this pathogen's variability (Wang et al. 2017).

Interestingly, in our study, just four races (ZD1, ZD3, ZD5, and ZE1) (Table 4) dominated the population of *M. oryzae* in HLJ throughout the period of study, indicating a degree of stability in the pathogen's race structure, although the f_{ti3ri} changed considerably from the first to second half of the period. These data infer that the core resistance genetics of the host remained stable and included the resistance genes *Pia*, *Pii*, and *Pik* that were all adopted from Japanese cultivars in 1970s in HLJ. That is, these cultivars have served as key parents in the local rice breeding programs for over five decades (Sun 2011; Zhang 2018; Zhang et al. 2017). Similar observations of the limited dominate races in the pathogen populations were reported in other groups (Liu et al. 2017; Mekwatanakarn et al. 2000; Wang et al. 2017).

Differential cultivar sets are founded on the principle of the gene-for-gene hypothesis (Atkins et al. 1967; Flor 1971; Kawasaki-Tanaka et al. 2016; Liu et al. 2017; Zhang et al. 2017). These cultivar sets provide data regarding the race or pathotype structure of the pathogen and also, what resistance genes/genotypes are being used or could be effective in local host cultivars (Liu et al. 2017; Zhang et al. 2017). Lei et al. (2011) recommended that cultivars grown in HLJ contain the genes *Pi9*, *Piz-5* (*Pi2*), *Pita-2*, *Pi12*, and *Pi20* based on the disease response of a set of 31 entries, each carrying a single major *M. oryzae* resistance gene, and a group of 12 popular local cultivars. Similarly, Kawasaki-Tanaka et al. (2016) reported that 16 resistance genes varied in their effectiveness against Japanese populations of *M. oryzae*. They reported that the presence of *Pit* ensured resistance against the full set of isolates tested; note that this gene was not fully effective against populations of *M. oryzae* found in China (Zhang et al. 2017). In the soybean root rot pathosystem, Dorrance et al. (2016) reported that none of the resistance genes involved in the 12 soybean differentials were effective against all of the isolates tested, but *Rps6* and *Rps8* were effective against the majority of isolates collected in northern regions of the sampled area in the United States. In the

stripe rust pathosystem, Liu et al. (2017) identified two resistance genes *Yr5* and *Yr15* from 18 monogenic differential lines, and both have conveyed stable resistance against the cognate pathogen since the 1960s in the United States.

In this research, we demonstrated that the dynamics of resistance within the CDCs could be divided into two types: the three *indica* entries expressed a higher resistance than the four *japonica* entries did (Table 5). The two entries Tetep and Zhenlong 13 seemed to be particularly promising donors of *M. oryzae* resistance for HLJ rice improvement programs, because they were resistant to most of the isolates tested. Based on the differential reactions of Sifeng 43 and Hejiang 18 as well as those of Zhenlong 13 and Dongnong 363, the presence of the two putative resistance genes α and ε was also confirmed (Table 5). Similarly, in our previous study, a total of five additional resistance genes, α to ε , were identified from the CDC based on spatial comparison of resistance performance among 7 CDCs and 12 Japanese differential cultivars with four populations of *M. oryzae* from China (Zhang et al. 2017) (Table 5). The three major resistance genes (*Pia*, *Pii*, and *Pik*) carried by the *japonica* subset of the CDCs might serve as a core of resistance in cultivars grown in HLJ over the whole period, because the four dominant races detected in 2006 to 2015 were responsible for reactions on the *japonica* subset carrying the three genes (Table 5). It would also be worthwhile to more thoroughly investigate the core of resistance within a given region and incorporate promising resistance genes into future cultivars to ensure a sustainable level of control over the disease (Dorrance et al. 2016; Liang et al. 2016; Lin et al. 2007; Mundt 2018).

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