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Comparison of disease resistance of maize varieties from the 1950s to the 2000s in China

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Abstract

The objective of this investigation was to analyze trends in diseases resistance along with genetic gain. Experimental materials consisted of maize varieties selected from each decade beginning with the 1950s. These varieties were evaluated for resistance to maize dwarf mosaic virus (MDMV), maize rough dwarf virus (MRDV), common smut disease (CSD) and head smut disease (HSD) in several different locations. Artificial inoculation was adopted for infection with MDMV and HSD, whereas natural infection was used for infection MRDV and CSD. Results indicated that resistance of the newer varieties to MDMV, CSD, and HSD was greater than that of older varieties, but the correlation to decades was not significant. To date, no variety tested in China has shown resistance to MRDV, which is likely due to a lack of maize germplasm resources resistant to MRDV in China. So the next goal will be to import new germplasm resources and select resistant germplasm as the basis of breeding resistant varieties.

Keywords: maize (*Zea mays* L), variety, disease resistance, era

Introduction

China is the second largest producer of maize (*Zea mays* L) in the world, with approximate 33 million ha sown and 178 million tons produced annually. The open-pollinated varieties (OPVs) grown extensively in China prior to the 1950s have been gradually replaced by double-cross hybrids since the 1960s. Single-cross hybrids began to be released in the 1970s, beginning with the hybrid Xindan-1 (Zhang et al, 2006; Tong, 2001). Since the 1950s, maize yield has increased greatly, particularly since the 1970s (Ci et al, 2011).

Recent genetic improvements in grain yield are due mostly to the increased stress tolerance of new hybrids that are able to withstand and thrive at increased plant densities (Duvick, 2005; Ci et al, 2011). Newer hybrids are more tolerant to stress than older hybrids when tested under low soil moisture (Dwyer et al, 1992), low soil N (Echarte et al, 2008), or excessive soil moisture (Duvick, 1997) in the field, and under controlled environmental conditions (Nissanka et al, 1997).

Tolerance to biotic stresses comprised of insects and diseases is also an important factor contributing to increased yield. A time series in Iowa from 1930 to 1991 following 36 hybrids and one OPV showed that there was a linear increase in resistance to second-generation European corn borer (ECB2) (Edmeades et al, 1997), even though there had been no direct selection for resistance to ECB2 (Duvick, 2005). Frei (2000) stated that the low-level presence of leaf diseases had a positive effect on yield performance of maize hybrids in northern Europe (Frei, 2000).

In this context it would seem that breeding for resistance, even if indirect, is also helpful for indirectly improving yield. However, disease prevalence changes over time. Dodd (2000) stated that during the past 40 years, the incidence of at least 14 maize diseases has significantly increased in the United States (Dodd, 2000), which indicates that plant disease susceptibility is an ongoing problem.

Likewise, in recent years in China, both long-standing and novel diseases have occurred at varying levels of prevalence, perhaps due to climate change. In northeastern China, HSD, CSD, and leaf spot disease were the most common diseases in recent years (Su et al, 2008). An HSD outbreak in northern China since 2000 has resulted in substantial yield loss (Xie et al, 2008). The area affected by CSD reached 1.8 million hm^2 in 2000 and has increased in recent years (E et al, 2006). MDMV and MRDV have now become prevalent in the Huabei region (Qiao et al, 2005). In 2005, MRDV occurred over a particularly large area of more than 733,000 ha and the harvest from more than 17,000 ha was completely lost (Xie et al, 2009). Each these were significant diseases in northern China, with highly negative impacts on maize production.

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Corn production losses have averaged 10%~20% due to diseases each year (Liu et al, 2000).

Although the replacement of varieties has occurred for many cycles since the 1950s, there has not been an emphasis on increased tolerance to biotic stress accompanied by genetic yield gains in China. Representative varieties from each decade since the 1950s were selected and evaluated for resistance to four diseases. The objective of this study was to analyze the trends in resistance to these diseases. to obtain valuable information for further yield improvement in China and elsewhere.

Materials and Methods

Maize Varieties

Thirty-four maize varieties released from 1950 to 2000, which were the most popular varieties from each decade in the main maize-growing areas in China, were tested in these experiments. The test panel includes four open-pollinated varieties (OPV), four double-cross hybrids, and 26 single-cross hybrids. Table 1 shows the release dates by decade and the heterotic backgrounds of these hybrids. Simple sequence repeat and pedigree analysis indicate that these hybrids belong to three heterotic populations (Xie et al, 2007) typically used in China : A, B, and D. Population A includes PA and Reid, from the United

Table 1 - List of varieties tested and their release dates.

Varieties	Decade	Parents (female × male)	Heterotic architecture
Jinhuanghou	1950s	OPV	
Jinhuanghou	1950s	OPV	
Baimaya	1950s	OPV	
Xiaolihong	1950s	OPV	
Yinglizi	1950s	OPV	
HD409	1960s	(WF9 × M14) × L289	
US13	1960s	(WF9 × 38-11) × (IllHy × L317)	
Weier156	1960s	(WF9 × Os420) × (M14 × CI187-2)	
Sishuang1	1960s	(Ying64×Tie84) × (M14×W20)	
Zhongdan2	1970s	Zi330 × Mo17	Lvda Redcob × Lancaster
Xindan1	1970s	525 × 517	Sipingtou × Lvda Redcob
Zhengdan2	1970s	Tangsipingtou × Huobai	Sipingtou × unknown
Qundan105	1970s	525 × C103	Lvda Redcob × Lancaster
Jidan101	1970s	Ji63 × M14	Reid × PA
Yedan4	1980s	U8112 × Huangzaosi	Reid × Sipingtou
Huang417	1980s	Huangzaosi × Mo17	Sipingtou × Lancaster
Shendan7	1980s	E28 × Shen5003	Lvda Redcob × PA
Danyu13	1980s	M017 × E28	Reid × Lvda Redcob
Yedan2	1980s	Ye107 × Huangzaosi	Reid × Sipingtou
Nongda60	1980s	Sheng5003 × Zong31	Reid × Lvda Redcob
Tiedan4	1980s	Ji63 × Zi330	PA × Lvda Redcob
Benyu9	1990s	7884Ht × Mo17Ht	Lvda Redcob × Lancaster
Jidan180	1990s	Ji853 × Mo17	Sipingtou × Lancaster
Yedan13	1990s	Ye478 × Dan340	Reid × Lvda Redcob
Sidan19	1990s	444 × Mo17	Sipingtou × Lancaster
Zhengdan14	1990s	478you × Zheng22	Reid × Lvda Redcob
Yedan19	1990s	Ye478 × Ye52106	PA × Lancaster
Jidan159	1990s	Ji846 × Dan340	Lancaster × Lvda Redcob
Nongda3138	1990s	P138 × Zong31	PB × Lvda Redcob
Nongda108	1990s	X178 × HuangC	PB × Reid
Ludan50	1990s	Luyuan92 × Qi319	Lancaster × PB
Zhengdan958	2000s	Zheng58 × Chang7-2	Reid × Sipingtou
Shendan16	2000s	Sheng137 × K12	PB × Sipingtou
Ludan981	2000s	9801 × Qi319	Sipingtou × PB
Denghai9	2000s	DH65232 × 8723	PB × Reid

Table 2 - Evaluation method for each disease.

Disease	Highly resistant (HR)	Resistant (R)	Mildly resistant (MR)	Susceptible (S)	Highly susceptible (HS)
MDMV	~0-10%	~10.1-25%	~25.1-30%	~30.1-40%	>40%
MRMV	~0-10%	~10.1-25%	~25.1-30%	~30.1-40%	>40%
HSD	~0-1.0%	~1.1-5.0%	~5.1-10.0%	~10.1-40.0%	>40%
CSD	~0-1.0%	~1.1-5.0%	~5.1-10.0%	~10.1-40.0%	>40%

States (Iowa Stiff Stalk Synthetic, Ames, IA). Population B includes PB and Lancaster, from the United States. The subpopulations PB and PA were selected from US commercial hybrids. Population D is composed of two subpopulations: Lvda Redcob and Sipingtou (Zhang et al, 2002).

Experimental Design

The experiment on MDMV resistance took place at the field experiment station at the Chinese Academy of Agricultural Sciences in Beijing in 2010. MDMV was rub-inoculated at the five-leaf stage (Kuntze et al, 1995). Virus inoculum was prepared from infected young plants by grinding leaves with mosaic symptoms into a homogenate in 0.01M phosphate buffer (pH 7.0) at a 1:10 (w:v) dilution and adding carborundum into the inoculum. After one week, inoculation was repeated.

The experiments on Maize Rough Dwarf Virus resistance took place at the field experiment station of Jining Agricultural Academy of Sciences. The sowing date was 28 May 2010. Outbreaks of MRDV, which have been very severe on the Huanghuai Plain in recent years, is transmitted by small brown planthoppers (*Laodelphax striatellus*) that arrive from the south and infect seedlings in early June. Severe natural infections occur reliably, so it is not necessary to inoculate plants with the virus.

The experiment on Head Smut Disease resistance took place in a field trail at the experiment station of the Plant Protection Institute, Jilin Agricultural Academy of Science in 2010. Before planting, HSD spores stored in the lab were made into a 0.1% inoculum with soil that was applied to the surface of the seeds (Su et al, 2008).

The experiments on Common Smut Disease resistance was carried out in the field at the experiment station of the Chinese Academy of Agricultural Sciences in Beijing in 2010. This field was severely infected with common smut disease annually, therefore, it was possible to take advantage of natural inoculation for this experiment.

In all the experiments, each plot consisted of two rows 4.0 m long with 0.60 m spacing, 0.25 m plant spacing, and three replications.

Evaluation methods

For MDMV and MRMV, evaluation methods included two steps. First, symptoms on each plant were recorded. Then, for MDMV, virus symptoms were evaluated during tasseling on a 0-5 scale, where 0 = symptomless; 1 = mild mosaic symptoms on ~1-2 upper leaves; 2 = mild mosaic symptoms on ~3-4 upper leaves; 3 = typical mosaic symptoms on all leaves above the cob and slightly dwarfed plant stature; 4 = typical mosaic symptoms on the entire plant, dwarfed stature and small ears; and 5 = significant mosaic symptoms, severely dwarfed, and no kernels on the ear. (Wang et al, 2006).

Then for MRMV, each plant was evaluated during the grain-filling period on a 0-4 scale, where 0 = healthy plant of normal height; 1 = up to 80% of healthy plant height and white areas on only several upper leaves; 2 = up to 66% of healthy plant height and symptoms appearing on the entire plant; 3 = up to 50% of healthy plant height and symptoms appearing on the entire plant; and 4 = less than 30% of healthy plant height and symptoms appearing on the entire plant (Miao et al, 2005).

For HSD and CSD, symptoms were evaluated during maturity. The number of plants with symptoms was recorded for each plot. The evaluation method is described as Wang et al (2006) in Table 2.

Infection status of the entire plot (variety) was represented as the disease index (DI). DI is a synthetical criterion which comprehensively taking both the infection rate and the severe extent into account. When the symptom was divided into different scale, DI = $\sum$ (score for each plant × number of plants) × 100/highest disease score × total number of plants). When only infection rate was recorded without scale, the DI was the percentage of infected plants (Wang et

Table 3 - ANOVA result for Disease index.

Source	MDMV			MRMV			HSD			CSD		
	Df	F	MS	Df	F	MS	Df	F	MS	Df	F	MS
Era	5	2.90	468.45*	5	0.30	35.10NS	5	0.72	71.98NS	5	3.67	359.47**
Type	2	5.61	905.11**	2	0.22	25.50NS	2	0.10	7.94NS	2	6.36	623.73**
Error	27			27			27			27		

MS: Mean Square; *Significant at the 0.05 level; **Significant at the 0.01 level; NS, not significant.

al, 2006).

The germplasm can then be divided into several severity groups according to DI (Wang et al, 2006). Evaluation method is outlined in Table 2.

Statistical analysis

Data analysis was conducted using SAS System for Windows (SAS, 2009). Treatments include three variety types (OPVs, double-cross hybrids, and single-cross hybrids) from six decades. ANOVA was conducted on the disease index between eras and between variety types, respectively, using PROC ANOVA for one-way classification.

Linear regression analysis (PROC REG) was used to examine the relationship between the evaluation index and the era of release.

Results

ANOVA results

As shown in Table 3, in the experiment on MDMV resistance, the ANOVA indicated significant differences among eras and extremely significantly differences among variety types. In the experiment on CSD resistance, ANOVA indicated extremely significant differences among both eras and variety types. To MRMV and HSD, the difference for eras and variety type were not significant.

Table 4 - Analysis of combined resistance to three diseases.

		MDMV		CSD		HSD	
Variety	Decade	DI	Evaluation	Percentage diseased plants	Evaluation	Percentage diseased plants	Evaluation
Baimaya	1950s	42.13	S	5.828	MR	7	MR
Jinhuanghou	1950s	36.00	MR	12.301	S	12.7	S
Xiaolihong	1950s	90.80	HS	42.133	HS	2.1	R
Yinglizi	1950s	53.54	S	3.783	R	3.7	R
HD409	1960s	30.65	MR	2.081	R	5.7	MR
Sishuang1	1960s	35.45	MR	8.284	MR	7	MR
US13	1960s	32.62	MR	3.55	R	1.8	R
Weier156	1960s	28.74	MR	6.26	MR	3.7	R
Jidan101	1970s	40.52	S	0.463	HR	0	HR
Qundan105	1970s	22.84	R	1.634	R	6.5	MR
Xindan1	1970s	30.37	MR	4.49	R	14.3	S
Zhengdan2	1970s	12.39	R	1.691	R	3.3	R
Zhongdan2	1970s	34.44	MR	2.737	R	39.3	S
Danyu13	1980s	32.94	MR	11.496	S	1.6	R
Huang417	1980s	30.79	MR	0	HR	1.6	R
Nongda60	1980s	43.27	S	3.354	R	1.7	R
Shendan7	1980s	43.14	S	2.282	R	11.9	S
Tiedan4	1980s	53.85	S	4.925	R	14.8	S
Yedan2	1980s	39.22	MR	1.334	R	15.9	S
Yedan4	1980s	43.30	S	4.934	R	0	HR
Benyu9	1990s	22.65	R	1.41	R	3.3	R
Jidan159	1990s	41.74	S	0.896	HR	3.6	R
Jidan180	1990s	54.94	S	0	HR	3.6	R
Ludan50	1990s	5.70	HR	2.085	R	1.9	R
Nongda108	1990s	30.64	MR	3.302	R	0	HR
Nongda3138	1990s	10.49	R	0	HR	3.2	R
Sidan19	1990s	49.28	S	0.422	HR	1.5	R
Yedan13	1990s	33.89	MR	16.272	S	2	R
Yeddan19	1990s	26.32	MR	48.644	HS	4.8	R
Yudan18	1990s	19.66	R	13.031	S	8.9	MR
Denghai9	2000s	31.11	MR	8.447	MR	0	HR
Ludan981	2000s	22.22	R	2.029	R	0	HR
Shendan16	2000s	20.37	R	0.412	HR	41.2	HS
Zhengdan958	2000s	41.27	S	1.205	R	15	S

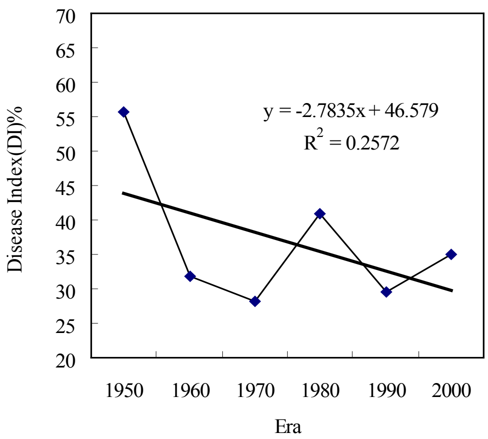

Figure 1 - Trends in disease index of MDMV among decades.

Evaluation of MDMV Resistance

The 34 varieties selected for this study exhibited significant differences in disease resistance during the MDMV evaluation (Table 4). Among the varieties tested, only Ludan50 from 1990s was highly resistant to MDMV. Seven hybrids were resistant to MDMV, including three from the 1990s (Benyu9, Nongda3138, Yudan18), two from the 2000s (Ludan981, Shendan16). These results indicated that hybrids from recent decades tended to be highly resistant to MDMV. Zhang et al (2008) reported that the inbred lines from PB population were highly resistant to MDMV. Among the resistant and highly resistant hybrids in the experiment, one of parental lines from Ludan50, Nongda3138, Ludan981 and Shendan16, were inbred lines of PB population (Table 1). Therefore the hybrids resistant to MDMV was result from the highly resistance of parental lines.

The average DI for each era was analyzed. The DI of varieties from the 1950s was far greater than that of varieties from other decades. No obvious differences in resistance existed among other eras. From 1950s to 1970s, the DI declined gradually. But in the 1980s and 2000s, the DI increased slightly (Figure 1). As found from the regression of DI on the era of release, the newer hybrids are apparently more resistant to MDMV than the older varieties.

Evaluation of Maize Rough Dwarf Virus Resistance

MRDV broke out severely in the Huanghuai Plains region in 2010, and is most severe around Jining in Shandong Province. It is vectored by the small brown planthopper described above. In early June, the first generation of small brown planthoppers swarm from the south. The sowing date for this experiment was 28 May 2010, and plants had reached the seedling stage in early June, so infection of these varieties by the virus was severe. All of the varieties tested are highly susceptible to MRMV. In addition, the DI of Nongda3138 was less than 50%, while that of others was above 80%. From these results, none of these varieties is currently resistant to MRMV.

Evaluation of Head Smut Disease Resistance

Among the 34 varieties tested, seven hybrids were highly resistant to CSD. These included Huang417, Jidan180, and Nongda3138, which were symptomless. Four varieties were susceptible to CSD, and two other varieties, Xiaolihong and Yedan19, were highly susceptible. All of the susceptible entries originated in the 1950s, the 1980s, and the 1990s (Table 4). In contrast, all of the varieties from the 1960s, the 1970s, and the 2000s were resistant to CSD.

The average incidence of infection in varieties from each decade was analyzed. Figure 2 shows that the infection rate for varieties from the 1950s was higher than that of other eras. Among the six eras, the percentage of infected plants in varieties from the 1970s was lowest. The newer varieties appeared to be more resistant to CSD than the older varieties.

Evaluation of Head Smut Disease Resistance

In Jilin, infection with HSD strain was accomplished by inoculation. Six hybrids were found to be free of symptoms. Three of these varieties were developed in the 2000s, and one was developed in the 1990s. Shendan16, which was developed in the 2000s, was highly susceptible to HSD (Table 4). Therefore, the performance of varieties from the 2000s was polarized: some were highly resistant, while others were highly susceptible or susceptible. All of the varieties tested from the 1990s were resistant to HSD. Bai et al (2010) found that the inbred lines Qi319, P138, HuangC, Zong31were highly resistant to HSD and K12 was highly susceptible to HSD. Qi319 was one of parental lines of Ludan50 (resistance) and Ludan981 (highly resistant). P138 and Zong31 were parental lines of Nongda3138 (resistant). HuangC was one of parental lines of Nongda108 (highly resistant). K12 was one of parental lines of Shendan16 (highly susceptible). Thus, the hybrids were resistant or susceptible to HSD because their

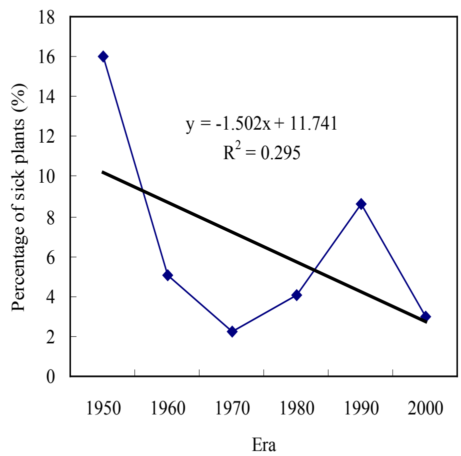

Figure 2 - Trends in the percentage of diseased plants with CSD with HSD among decades.

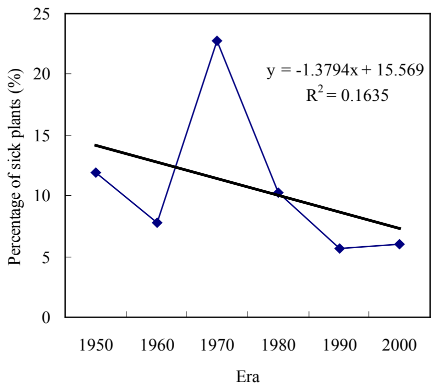

Figure 3 - Trends for the percentage of diseased plants among decades in Jilin.

parental lines were highly resistant or highly susceptible to it.

The average percentage of infected plants among varieties developed in each era was analyzed. As shown in Figure 3, the proportion of infected plants among varieties from the 1970s was highest, and that among varieties from the 1990s was lowest. Although the infection rate increased again in varieties from the 2000s, as a whole, infection rates tended to decline over the decades such that the newer varieties were more resistant to HSD than the older ones.

Analysis of combined resistance to three diseases

Because all of the varieties tested here were highly susceptible to MRDV, multiple resistance to other diseases (MDMV, CSD, and HSD) was analyzed (Table 4). Four varieties, three from the 1990s and one from the 2000s had superior combined resistance. The varieties with moderate resistance to multiple diseases were Denghai9, Nongda108, Huang417, Sishuang1, HD409, and Weier156, three of which were from the 1960s. The varieties with least resistance to multiple diseases were Tiedan4, Shendan7, Jinhuanghou, and Xiaolihong, which were susceptible to two diseases. Jinhuanghou and Xiaolihong are varieties that were developed in the 1950s, among which resistance to multiple diseases was apparently lower relative to other decades.

Discussion

Breeding for resistance or tolerance to MRDV

MRDV is transmitted by a small brown planthopper (*Laodelphax striatellus*) whose population levels have been abnormally large in recent years in northern China (Wang et al, 2011). The emergence of diseases is often encouraged by changes in cultural practices and by widespread planting of a single genotype (Duvick, 2005). In this paper, all of the varieties tested have been highly susceptible to MRDV (Table 3). This would indicate that the prevalence of MRDV has partly resulted from a deficiency of resistant varieties, so the breeding of good MRDV-resistant hybrids will be necessary to mitigate future crop losses.

Because there is no completely immune germplasm, and highly resistant germplasm resources are scarce in this region, screens for resistant germplasm have been initiated. A few inbreds from the PB heterotic population, including Qi319, Shen137, X178, were moderately resistant to MRDV, while other populations were susceptible (Xie et al, 2009; Yang et al, 2010; Huang et al, 2011). Lu et al (2001) found that some inbreds introduced from America were highly resistant, while Wang et al (1998) found that some local varieties were resistant to MRDV. It is apparent that collection and utilization of both local and exotic germplasm should be emphasized during screening for resistant germplasm resources.

The next important objective will be to breed resistant inbred lines. If resistant germplasm is well-adapted to local climate, it will be possible to directly select and create inbred lines from them. Alternatively, unadapted resistant germplasm could be used to improve current selection lines. Currently, breeders often utilize foreign material as sources of favorable genes to introgress into and improve elite inbred lines, instead of developing new inbred lines from exotic germplasm.

Finally, crosses will be made between one or more highly resistant parents to obtain hybrids. Although one parent from the PB population was moderately resistant, the progeny of its crosses, such as Ludan50, Ludan981, were often susceptible (Table 3). The best combination for crosses would be a pair of highly resistant inbred lines.

Analysis of Resistance to Multiple Diseases

We analyzed combined resistance to MDMV, CSD, and HSD, with the result that Ludan50, Nongda3138, Ludan981, and Benyu9 were each found to be resistant to all three diseases. The performance of these hybrids in terms of resistance was determined by the genotypes of the parents.

There has been a significant amount of research on resistance to these diseases in maize germplasm. Kutze et al (1997) studied the resistance of European germplasm to MDMV and found that seven dent inbreds were resistant, while all of the flint inbreds tested were susceptible. (Shi et al, 2003) stated that in China, the PB population was highly resistant to MDMV; the sipingtou population was moderately resistant; and other populations were susceptible. Inbred lines from PB population were highly resistant, and the PA, Lancaster and Lvda Redcob populations were resistant to HSD (Gao et al, 2006; Xie et al, 2008; Tong, 2001). The PB population, to which Ludan50, Nongda3138, and Ludan981 are related (Table 1), contains resistance to many diseases prevalent in China.

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