Genetic Diversity and Gene Flow Observed in Two Cereal Aphid (Hemiptera: Aphididae) Species and Populations in the Chinese Corn Belt Region[1]

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Abstract The cereal aphids, *Rhopalosiphum maidis* (Fitch) and *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), are serious pests of maize, *Zea mays* L., globally. Basic information about the genetic structure of these aphids is unknown. We, therefore, estimated the genetic diversity and genetic flow from partial fragments of the mitochondrial cytochrome oxidase I gene collected from different geographic populations of aphids throughout the Songliao Plain of northeastern China. Our analysis of a 425-bp sequence on 297 *R. maidis* and 287 *R. padi* individuals revealed 17 and 3 variable sites, respectively. Fifteen haplotypes were obtained among the *R. maidis* populations, and only haplotype RM1 was shared. Three shared haplotypes were obtained among the *R. padi* populations. No obvious geographical trends were detected based on the haplotype network and neighbor-joining tree. Relatively low haplotype diversity indices were observed in the *R. maidis* populations (haplotype diversity [Hd] = 0.14207, average number of nucleotide differences [K] = 0.17340, and nucleotide diversity [Pi] = 0.00041), whereas relatively high haplotype diversity indices were observed in the *R. padi* populations ($Hd = 0.53249$, $K = 1.46614$, and $Pi = 0.00345$). There was moderate gene flow (number of migrants [Nm] = 2.33) among *R. maidis* populations, but there was low gene flow ($Nm = 0.82$) among *R. padi* populations. Analysis of molecular variance showed high genetic differentiation within populations. Genetic distance and geographic distance were not significantly associated according to the Mantel test. The results suggest that the difference in the aphids' existence strategies has resulted in a different mitochondrial evolution pattern in the Songliao Plain region, and they provide a foundation for accurately forecasting systems against this pest.

Key Words cereal aphid, molecular marker, haplotype, genetic differentiation, migration

Maize (*Zea mays* L.) is a major cereal crop in Jilin Province, located in the center of the Songliao Plain in northeastern China. In this area, about 3.8 million ha of maize is grown for food, animal feed, and fuel. This area possesses the highest number of crop exports in the country and is considered to be the "Chinese Golden Corn Belt." In this region, maize is severely affected by a plethora of insect pests (Sun et al. 2020). Among them, cereal aphids are major pests that cause severe damage to all stages of growth and development of maize. This species is a sap-sacking pest that has a worldwide distribution and has contributed to serious

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economic losses to maize in the United States, Canada, Spain, Slovakia, Turkey, and other countries (Savaris et al. 2013, Klein and Smith 2020, Hu et al. 2021). There are three major aphid species, namely, *Rhopalosiphum maidis* (Fitch), *Rhopalosiphum padi* (L.), and *Aphis gossypii* Glover (Hemiptera: Aphididae), impacting maize production in the Golden Corn Belt. *Rhopalosiphum maidis* and *R. padi* are the most commonly occurring aphid species in cereal production; both have a worldwide distribution (Foott 1977, Varsani et al. 2019, Stewart et al. 2020). Both nymphs and adults directly damage maize. The pest also transmits several plant viruses (Stalmachová and Cagán 2001, Karami et al. 2016).

Winters on the Songliao Plain are harsh for most insects. Generally, the life cycles of *R. maidis* and *R. padi* are almost identical. In the growing season, the aphids emigrate from overwintering on other plants (e.g., *Prunus*) to maize. As the crop approaches harvest in the autumn, temperatures decrease. The winged aphids appear and emigrate from the maize field to suitable overwintering habits. However, there are some different biological behaviors between the two species. The corn leaf aphid, *R. maidis*, is a polyphagous insect. When it migrates to the maize field in late July, the pest settles inside the whorl formed by young leaves. Only when the tassel becomes exposed, the pest transfers into ears of corn. The bird cherry-oat aphid, *R. padi*, is also a polyphagous insect with a wide host range and is one of the serious wheat pests in southern China. It emigrates to the maize field early (e.g., mid-June) and is widely distributed over the host maize plant where it damages whorl leaves, immature tassels, flower buds, and young leaves.

Due to the heavy damage inflicted by these species, their morphology, biology, genome sequence, karyotype variation, natural enemies, and maize host plant resistance have been substantially studied (Brown and Blackman 1988, Toft et al. 1995, Bayhan 2010, Meihls et al. 2013, Louis et al. 2015, Wang et al. 2018). In addition, there are some preliminary studies of molecular markers in *R. maidis* and *R. padi* in other countries (Martinez-Torres et al. 1997, Simon et al. 2001, Rakauskas et al. 2014).

The Chinese Golden Corn Belt is a special area due to the topography and extensive maize cultivation. An analysis of the population structure of the two maize pest species could not only reveal population differentiation but also provide valuable information on the relationship between genetic diversity and biological behavior. Molecular markers, such as mitochondrial DNA (mtDNA), are very useful in the evaluation of genetic structure and gene flow. Different fragments of cytochrome oxidase I gene (COI) evolve at different rates, which make it effective for animal evolutionary analyses (Lunt et al. 1996). In this study, we collected samples across Jilin Province and then used partial sequences of mtDNA COI to investigate the genetic diversity and genetic variation of these species. Such studies could increase our understanding of the species evolutionary pattern and provide valuable knowledge for maize cultivation countries at similar latitudes (e.g., United States and Ukraine).

Materials and Methods

Sampling. *Rhopalosiphum maidis* ($n = 297$) and *R. padi* ($n = 287$) specimens were collected from maize fields in August of 2019 (Table 1; Fig. 1). Experimental

Table 1. Samples examined in this study.

Population Code	Collecting Locality	Geocoordinates	Sampling Size	
			R. maidis	*R. padi*
YS	Yushu	44.5034112°N, 126.3442461°E	30	28
CL	Changling	44.1720322°N, 124.1973324°E	30	30
DH	Dunhua	43.2150598°N, 128.0949287°E	30	26
Dh	Dehui	44.3190824°N, 125.5920382°E	30	28
FS	Fusong	42.2209819°N, 127.1740371°E	30	19
FY	Fuyu	45.0197332°N, 126.0950983°E	30	25
GZL	Gongzhuling	43.5358333°N, 124.8244444°E	29	27
JL	Jilin	43.5644283°N, 126.2284228°E	29	26
LS	Lishu	43.3475174°N, 124.3472222°E	30	19
QA	Qianan	44.5146182°N, 124.0246667°E	29	29
TN	Taonan	45.3316666°N, 122.8530555°E	—	30

—, represents no data collected.

method and statistical analyses were the same for both species. Following morphological identification, all the specimens were preserved in 100% ethanol and frozen at –20°C. Total genomic DNA was extracted using a genomic DNA purification kit (Sangon Biotech, Shanghai, China).

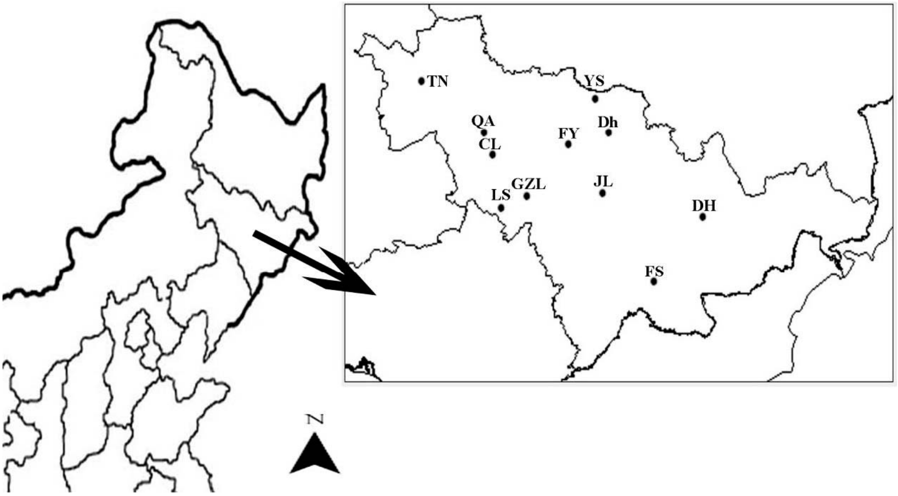

Fig. 1. Sample location of *R. maidis* and *R. padi* in the Jilin Province.

Polymerase chain reaction (PCR). Previous studies successfully utilized partial COI sequences in aphids (Wongsa et al. 2017). A 440-bp fragment of the mtDNA COI gene was amplified using the primers C1-J-1751 and C1-N-2191 that were designed by Simon et al. (1994). Each PCR mixture contained 2 μl of DNA template (40–100 ng), 1 μl of each primer (10 μM), 1 μl of deoxynucleoside triphosphate (10 mM), 2.5 μl of Taq buffer (10×), 0.2 μl of TaqDNA polymerase (5U/μl), and distilled water, making a final volume of 25 μl. The reactions were performed in a Veriti 96-well instrument (Applied Biosystems, Foster City, CA, USA). The PCR conditions were as follows: (a) 95°C, 5 min; (b) 94°C, 30 s; (c) 58°C, 30 s; (d) 72°C, 1 min; (e) cycle to step b, 38 times; (f) 72°C, 10 min; and (g) 4°C, final hold. PCR products were purified and sequenced using a 3730 automatic DNA sequencer (Applied Biosystems). Primer sequences were as follows: C1-J-1751, 5′-GGATCACCTGATATAGCATTCCC-3′; and C1-N-2191, 5′-CCCGGTAAAATTAAAATATAAACTTC-3′.

Statistical analyses. The COI sequences obtained in this study were submitted to the National Center for Biotechnology Information (NCBI) database. These sequences were edited and aligned using Chromas and DNAMAN. MEGA 4.0 (Tamura et al. 2007) was used to calculate the nucleotide compositions and variable sites. Genetic distance and neighbor-joining (NJ) tree were also performed using this software. For phylogenetic analysis, a median-joining network among the COI haplotypes was constructed using Network 4.6.1.6 (Bandelt et al. 1999). Genetic variation was investigated as haplotype diversity (*Hd*), nucleotide diversity (*Pi*), the average number of nucleotide differences (*K*), gene flow estimates, and Tajima' *D* (Tajima 1989) by using the DNASP5 program (Librado and Rozas 2009). Using GenAlex6.41 software, a Mantel test was used to analyze the correlation between genetic distance and geographical distance (Peakall and Smouse 2006). Analysis of molecular variance (AMOVA) was estimated using Arlequin 3.5.1.2 (Excoffier et al. 2005).

Results

Base composition. For *R. maidis*, sequences were identified via comparison with a previously submitted sequence from the NCBI database (accession no. KF022221.1). The alignment of the COI sequence contained 425 bases in the final set with 408 conserved sites. Of the 17 variable sites, 16 were single variable sites and 1 was a parsimonious informative site. The average base composition was as follows: T, 40.8%; C, 15.2%; A, 33.3%; and G, 10.6%. There were 15 transitions and 2 transversions. The observed transition:transversion ratio was 7:9. For *R. padi*, sequences were identified via comparison with a previously submitted sequence from the NCBI database (accession nos. MT119781.1). The alignment of the COI sequence contained 425 bases in the final set with 422 conserved sites and 3 single variable sites. The average base composition was as follows: T, 40.8%; C, 14.7%; A, 33.9%; and G, 10.6%. There were three transitions. The nucleotide composition of the *R. maidis* and *R. padi* sequences showed that no insertions or deletions were observed. The sequence was strongly A-T biased as observed in other insects.

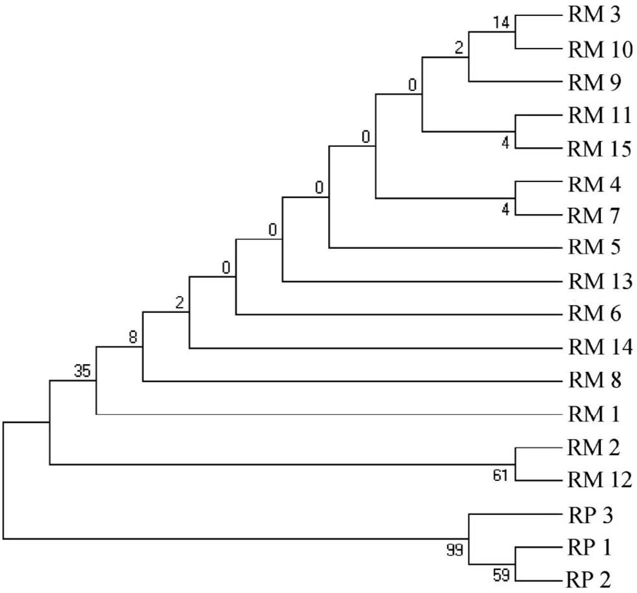

Fig. 2. Phylogenetic relationships of *R. maidis* and *R. padi* based on NJ analysis of the COI haplotypes. Bootstrap values were generated from 1,000 replicates.

Haplotypes. For *R. maidis*, a total of 15 unique haplotypes (RM1–RM15) were detected. All the sequences were deposited in GenBank (accession nos. MN929098–MN929112). The average distance between haplotypes was 0.06, ranging from 0.002 to 0.012. Haplotype RM1 was detected in all the populations and had the highest amount (i.e., accounted for 92.59% of haplotypes). It is likely to be the ancestral haplotype. No genotype was shared among the other haplotypes. Haplotype RM15 was the second most frequent haplotype (3.03%), which was found in nine individuals and was only present in the Qianan, China, population. The remaining haplotypes were only found once in different populations. For *R. padi*, a total of three unique haplotypes (RP1–RP3) were detected. All the sequences were deposited in GenBank (accession nos. MW455104–MW455106). The average distance between haplotypes was 0.005, ranging from 0.002 to 0.007. Haplotype RP3 was detected in all the populations and had the highest amount (i.e., accounted for 56.1% of haplotypes). Haplotype RP1 was the next most common haplotype (39.02%), which was not found in only in the Taonan, China, population. Haplotype RP2 was shared among four populations (Changling, Dehui, Fusong, and Jilin). The RM1 and RP3 sequence contained 32 variable bases (7.5%). The phylogenetic tree and network defined the haplotypes into two groups (*R. maidis* group and *R. padi*) (Figs. 2, 3). For both species, there was no evidence for a strong geographical pattern corresponding to the studied haplotypes based on the haplotype network and NJ tree (Figs. 2, 3).

Genetic diversity. The summary of *Hd* indices of *R. maidis* and *R. padi* from Jilin Province are given in Table 2. For *R. maidis*, a relatively low level of diversity

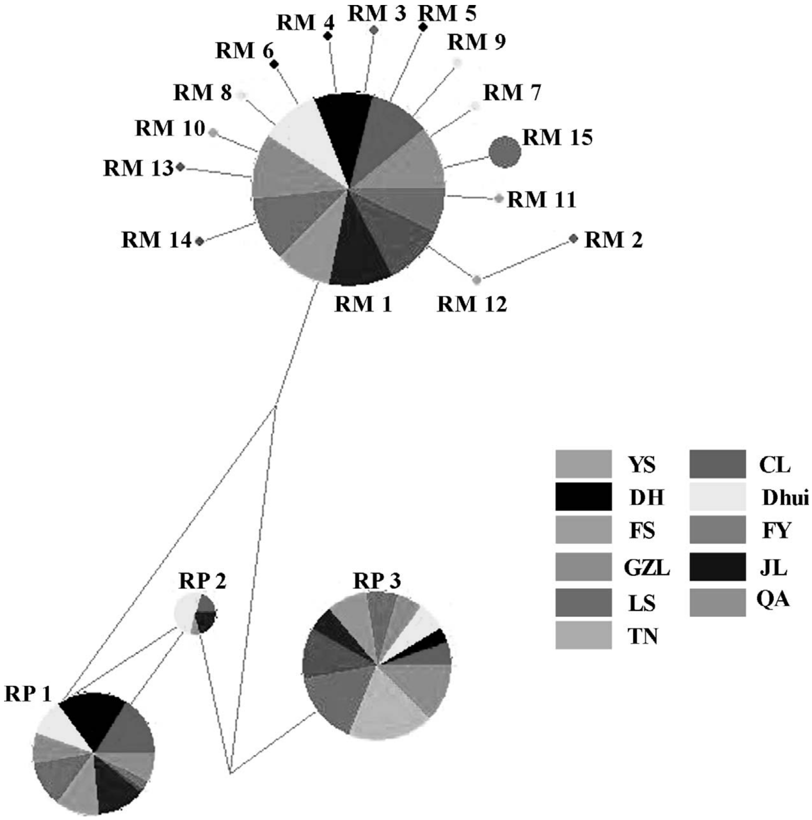

Fig. 3. mtDNA haplotype network in the examined populations of *R. maidis* and *R. padi*. Different circles represent different haplotypes, and the circle size is proportional to the sample size. Different colors represent different geographical groups.

was detected among the populations. Overall, the *Hd*, *K*, and *Pi* of all samples were 0.14207, 0.17340, and 0.00041, respectively. The average number of haplotypes (*H*) was 2.4 and ranged from 1 to 4. The values of *Hd* ranged from 0 to 0.44335, with an average value of 0.12911. The values of *K* ranged from 0 to 0.44335, with an average value of 0.15858. The values of *Pi* ranged from 0 to 0.00104, with an average value of 0.00037. For *R. padi*, a relatively high level of diversity was detected among the populations. Overall, the *Hd*, *K*, and *Pi* of all samples were 0.53249, 1.46614, and 0.00345, respectively. The values of *H* were 2.2 and ranged from 1 to 3. The values of *Hd* ranged from 0 to 0.67989, with an average value of 0.40845. The values of *K* ranged from 0 to 1.57895, with an average value of 1.09789. The values of *Pi* ranged from 0 to 0.00372, with an average value of 0.00263. For both species, the overall values of Tajima's *D* were significantly negative, which suggests a recent population expansion in Jilin Province.

Table 2. Summary of haplotype diversity indices of the mtDNA COI gene.

	Number of Haplotypes (*H*)		Haplotype Diversity (*Hd*)		Nucleotide Diversity (*Pi*)		Average Number of Nucleotide Differences (*K*)		Tajima's *D*		Statistical Significance	
Population	***R. maidis***	***R. padi***	***R. maidis***	***R. padi***	***R. maidis***	***R. padi***	***R. maidis***	***R. padi***	***R. maidis***	***R. padi***	***R. maidis***	***R. padi***
YS	1	2	0	0.42328	0	0.00299	0	1.26984	—	1.55354	—	$P > 0.10$
CL	3	3	0.13103	0.55862	0.00063	0.00321	0.26667	1.36552	−1.88948	1.89027	$P < 0.05$	$0.10 > P > 0.05$
DH	4	2	0.19310	0.32308	0.00063	0.0028	0.26667	0.96923	−1.88948	0.5714	$P < 0.05$	$P > 0.10$
Dh	4	3	0.19310	0.67989	0.00047	0.0034	0.20000	1.44709	−1.73178	2.10545	$0.10 > P > 0.05$	$P < 0.05$
FS	1	3	0	0.57895	0	0.00372	0	1.57895	—	2.28287	—	$P < 0.05$
FY	1	2	0	0.51333	0	0.00362	0	1.54	—	2.33033	—	$P < 0.05$
GZL	4	2	0.19951	0.51852	0.00065	0.00366	0.27586	1.55556	−1.88946	2.42291	$P < 0.05$	$P < 0.05$
JL	1	3	0	0.6	0	0.00343	0	1.45846	—	2.09847	—	$P < 0.05$
LS	3	2	0.13103	0.10526	0.00031	0.00074	0.13333	0.31579	−1.50738	−1.7188	$P > 0.10$	$0.10 > P > 0.05$
QA	2	2	0.44335	0.19212	0.00104	0.00136	0.44335	0.57635	−2.34219	−0.5834	< 0.01	$P > 0.10$
TN	—	1	—	0	—	0	—	0	—	—	—	—
Total	15	3	0.14207	0.53249	0.00041	0.00345	0.17340	1.46614	−2.34219	3.11772	$P < 0.01$	$P < 0.01$

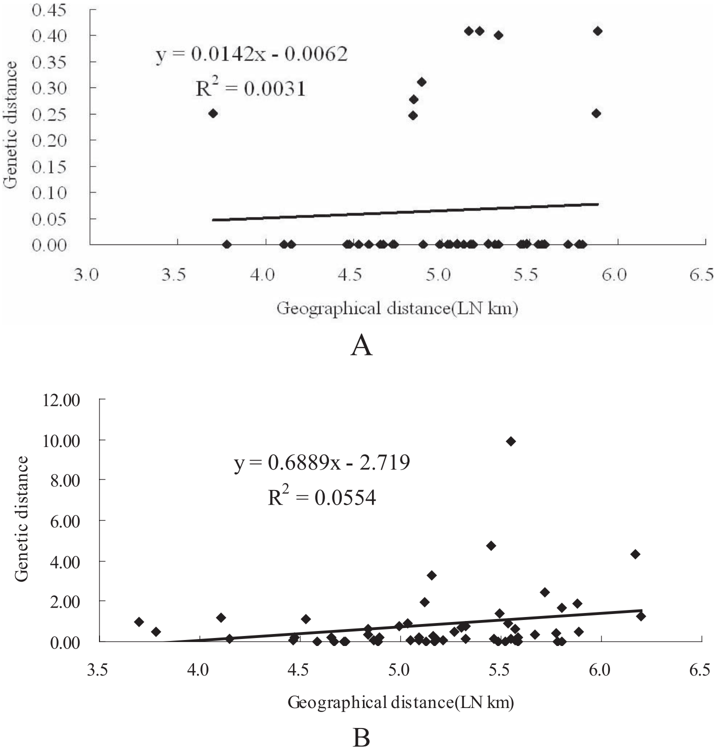

Fig. 4. Correlation analyses between geographic distance and genetic distance based on COI data. (A) *R. maidis*. (B) *R. padi*.

Genetic variation. For *R. maidis*, there was moderate gene flow (*Nm* = 2.33) among populations. The pairwise *Kxy* ranged from 0 to 0.44828, with an average value of 0.17627. The pairwise *Dxy* ranged from 0 to 0.00105, with an average value of 0.00041 (Table 3). The pairwise *Fst* ranged from −0.00855 to 0.28571, with an average value of 0.04851. The pairwise *Gst* ranged from −0.00825 to 1, with an average value of 0.16364 (Table 4).

For *R. padi*, there was relatively low gene flow (*Nm* = 0.82) among populations. The pairwise *Kxy* ranged from 0.15789 to 2.42308, with an average value of 1.50105. The pairwise *Dxy* ranged from 0.00037 to 0.0057, with an average value of 0.00353 (Table 5). The pairwise *Fst* ranged from −0.04416 to 0.8, with an average value of 0.22778. The pairwise *Gst* ranged from −0.0197 to 0.68183, with an average value of 0.14269 (Table 6). For both species, the results of the AMOVA test revealed that most of the differences occurred within populations (*R. maidis*, 90.09%; *R. padi*, 65.69%), whereas smaller variance occurred among populations (*R. maidis*, 9.91%; *R. padi*, 34.31%). There was no significant correlation of genetic distance with geographical distance by the Mantel test (*R. maidis*, R = 0.056, *P* = 0.19; *R. padi*, R = 0.235, *P* = 0.06) (Fig. 4).

Discussion

We confirmed that the populations of *R. maidis* and *R. padi* in Jilin Province of China underwent a recent population expansion as indicated by Tajima's D. Increased planting of maize during the last century is likely responsible.

The genetic fragment analyzed in our study contains the partial COI region, which is applicable to population genetic studies (Anstead et al. 2002, Yukuhiro et al. 2011, Criado and Fernández 2014, Rakauskas et al. 2014, Wongsa et al. 2017). There were 17 variable sites in the *R. maidis* population and 3 variable sites in the *R. padi* population. It seems that there was not a variety of variable sites, which may be due to the short population expansion history and similar ecological environment. Otherwise, another possible explanation is the conservatism of the gene fragment in this species. Although the variable sites are not plentiful, the findings provide a sufficient basis for our deductions and conclusions.

We used the same gene fragment in the same genera status, but the two aphid populations differed in their evolutionary pattern. For *R. maidis* populations, 15 haplotypes were obtained from different sampling locations. No shared haplotypes were detected, excluding the ancestral haplotype. From the central haplotype RM1, 14 haplotypes were identified as exclusive. The results indicated that haplotype RM1 has a stronger survival advantage in the Golden Corn Belt. The centric-haplotype is well adapted to the local environment. The phenomenon also was found in other reports (Meriam et al. 2015, Thirumaraiselvi and Thangaraj 2015, Wang et al. 2017). By comparison, three shared haplotypes were detected in the *R. padi* population. The population consisted of two widely distributed haplotypes, which were present at almost all locations and suggests that a mixed population existed with the environment. Altogether, these haplotypes exhibited a weak geographical clustering. A different existence strategy has resulted in a different mitochondrial evolution pattern.

The genetic diversity of aphid populations is lower than pests with higher observed dispersal rates, such lepidopterans or nonmigratory grasshoppers (Sun et al. 2015, Li et al. 2019). However, the result was caused by body type. The body size of aphids is small and can only accommodate a relatively short displacement distance due to their physical flight ability. Both relatively low and high genetic diversity values were recorded in aphid species (Puterka et al. 1993, Simon et al. 1996, Criniti et al. 2006, Charaabi et al. 2008, Samuel et al. 2014). Low levels of genetic diversity were found in *R. maidis* populations. The value was likely associated with their pest status and biological behavior. The distributional area of *R. maidis* is limited inside the whorl for an extended period of time. By contrast, a relatively high genetic diversity was observed in *R. padi* populations. The results are also associated with the species pest status and biological behavior. In contrast to *R. maidis*, *R. padi* exhibits a wider spatial distribution, and appeared on almost all parts of the maize plant.

Genetic diversity is an important indicator of environmental adaption (Mooney 2011, Hojas et al. 2020). High value of genetic diversity enabled *R. padi* survival when faced with deteriorating environmental conditions. There was a serious typhoon disaster in Jilin Province in September 2020. Corn suffered severe

Table 3. Pairwise *Kxy* (upper diagonal) and *Dxy* (lower diagonal) values of the partial COI gene of *R. maidis* populations in the Jilin Province.

	YS	CL	DH	Dh	FS	FY	GZL	JL	LS	QA
YS	—	0.13333	0.13333	0.1	0	0	0.13793	0	0.06667	0.31034
CL	0.00031	—	0.26667	0.23333	0.13333	0.13333	0.26897	0.13333	0.2	0.44368
DH	0.00031	0.00063	—	0.23333	0.13333	0.13333	0.27126	0.13333	0.2	0.44368
Dh	0.00024	0.00055	0.00055	—	0.1	0.1	0.23793	0.1	0.16667	0.41034
FS	0	0.00031	0.00031	0.00024	—	0	0.13793	0	0.06667	0.31034
FY	0	0.00031	0.00031	0.00024	0	—	0.13793	0	0.06667	0.31034
GZL	0.00032	0.00063	0.00064	0.00056	0.00032	0.00032	—	0.13793	0.2046	0.44828
JL	0	0.00031	0.00031	0.00024	0	0	0.00032	—	0.06667	0.31034
LS	0.00016	0.00047	0.00047	0.00039	0.00016	0.00016	0.00048	0.00016	—	0.37701
QA	0.00073	0.00104	0.00104	0.00097	0.00073	0.00073	0.00105	0.00073	0.00089	—

Table 4. Pairwise *Fst* (upper diagonal) and *Gst* (lower diagonal) values of the partial COI gene of *R. maidis* populations in the Jilin Province.

	YS	CL	DH	Dh	FS	FY	GZL	JL	LS	QA
YS	—	0	0	0	0	0	0	0	0	0.28571
CL	0.0087	—	0	0	0	0	−0.00855	0	0	0.19985
DH	0.01754	−0.00642	—	0	0	0	0	0	0	0.19985
Dh	0.01754	−0.00642	−0.0081	—	0	0	0	0	0	0.21609
FS	1	0.0087	0.01754	0.01754	—	0	0	0	0	0.28571
FY	1	0.0087	0.01754	0.01754	1	—	0	0	0	0.28571
GZL	0.01849	−0.00626	−0.00822	−0.00822	0.01849	0.01849	—	0	0	0.1978
JL	1	0.00855	0.01726	0.01726	1	1	0.01818	—	0	0.28571
LS	0.0087	−0.00825	−0.00642	−0.00642	0.0087	0.0087	−0.00626	0.00855	—	0.23519
QA	0.16902	0.10829	0.08809	0.08809	0.16902	0.16902	0.0857	0.16667	0.10829	—

Table 5. Pairwise *Kxy* (upper diagonal) and *Dxy* (lower diagonal) values of the partial COI gene of *R. padi* populations in the Jilin Province.

	YS	CL	DH	Dh	FS	FY	GZL	JL	LS	QA	TN
YS	0	0.00403	0.00446	0.00371	0.00356	0.00371	0.00347	0.00388	0.00218	0.00233	0.00202
CL	1.71429	0	0.00281	0.00331	0.00349	0.00339	0.00357	0.00322	0.00458	0.00446	0.00471
DH	1.8956	1.19231	0	0.00327	0.00349	0.00327	0.00361	0.00303	0.00547	0.00525	0.0057
Dh	1.57653	1.40714	1.39011	0	0.00348	0.00348	0.00354	0.00334	0.00391	0.00386	0.00395
FS	1.51128	1.48421	1.48381	1.47932	0	0.00352	0.00353	0.0035	0.00358	0.00358	0.00359
FY	1.57714	1.44	1.38923	1.47857	1.49684	0	0.00355	0.00343	0.00391	0.00387	0.00395
GZL	1.47619	1.51852	1.53419	1.50661	1.50097	1.50667	0	0.00356	0.00341	0.00343	0.0034
JL	1.64835	1.36923	1.28698	1.42033	1.48583	1.45846	1.51282	0	0.00426	0.00418	0.00434
LS	0.92481	1.94737	2.32591	1.65977	1.52355	1.66105	1.45029	1.80972	0	0.00102	0.00037
QA	0.99015	1.89655	2.2321	1.64163	1.52087	1.64276	1.45594	1.77454	0.43557	0	0.00073
TN	0.85714	2	2.42308	1.67857	1.52632	1.68	1.44444	1.84615	0.15789	0.31034	0

Table 6. Pairwise *Fst* (upper diagonal) and *Gst* (lower diagonal) values of the partial COI gene of *R. padi* populations in the Jilin Province.

	YS	CL	DH	Dh	FS	FY	GZL	JL	LS	QA	TN
YS	0	0.11102	0.2562	0.06845	0.02513	0.05793	0.02202	0.07896	0.06779	0.03526	0.1533
CL	0.23135	0	0.0184	0.01034	0.00078	–0.00353	0.0155	–0.01544	0.30458	0.27941	0.42958
DH	0.4094	0.02091	0	0.09959	0.079	0.05112	0.09678	0.03852	0.54237	0.4884	0.68183
Dh	0.13832	0.0006	0.13089	0	0.00243	0.02135	0.02155	–0.00307	0.21143	0.19043	0.31549
FS	0.05749	0.00807	0.14134	–0.02278	0	–0.01784	–0.0197	–0.01161	0.21212	0.16387	0.33423
FY	0.1092	–0.00886	0.0969	–0.01013	–0.04184	0	–0.01341	–0.00951	0.26262	0.22142	0.39202
GZL	0.04301	0.03818	0.17716	0.00351	-0.04416	-0.02729	0	0.00179	0.19342	0.15666	0.3109
JL	0.17241	-0.03123	0.05683	–0.02284	–0.02213	–0.02795	0.00384	0	0.26669	0.23556	0.38724
LS	0.14273	0.56831	0.72376	0.46894	0.37818	0.44138	0.35484	0.5098	0	–0.00976	0.00108
QA	0.06772	0.48805	0.65378	0.38371	0.29143	0.35585	0.26786	0.42666	–0.02411	0	0.03765
TN	0.25926	0.65862	0.8	0.56895	0.48276	0.54167	0.46154	0.605	0	0.07143	0

damage, and almost no insects appeared in our experiment field. However, *R. padi* also was observed after the disaster, which shows their strong adaptability.

Because of the plain's topography, there were no effective geographical barriers in the region, which make migration and population exchange feasible. Our results confirmed that hypothesis. The median-joining network and haplotype network showed no apparent geographical structure in this study. In addition, the lack of a pattern was observed between genetic and geographical distance by the Mantel test. For the *R. maidis* population, the *Nm* values of 2.33 ($>$1.0) among the populations in our study suggested a moderate rate of gene flow. Such gene flow may be explained by the long-distance migration behavior of the species. Possible migration in aphids was recorded by Isard et al. (1990) and Riley et al. (1995). Some aphid species can undertake windborne migrations over ranges of hundreds of kilometers (Reynolds et al. 1999). Rose et al. (1975) also documented an intermediate-range migration by *R. maidis*. The species host transfer migration occurs in late July. During that period, the wind is optimal for insects to migrate (Sun et al. 2018). If the aphid moves with summer seasonal winds, it could undertake windborne migration. The movements may have led to a widespread redistribution of beneficial gene flow among the populations in the plain. Gene flow also can reduce genetic divergence. AMOVA results for *R. maidis* confirmed that low genetic variation occurred among populations. In comparison, the *Nm* values of 0.82 ($<$1) among the *R. padi* populations in our study suggested a low rate of gene flow. For this reason, the low value might be caused by low migration frequency. Although *R. padi* is a migratory species (Nottingham et al. 1991, Luo et al. 1994, Hansen 2010), they reach the maize field in an earlier period, and the corn belt provides sufficient food. Therefore, the adequate resources reduce the need for migration and have resulted in a decrease in gene flow. Moreover, AMOVA results for *R. maidis* confirmed that larger genetic variation occurred among populations. It was postulated that the variation will form a subpopulation. Future experiments should examine this scientific problem.

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