Distribution of *Phytophthora infestans* Populations in Seven Asian Countries*

Ryo NISHIMURA**, Kaori SATO**,***, Wang Hyu LEE†, U.P. SINGH††,
Tun-tsChu CHANG††, Euis SURYANINGSIH‡, Somkiat SUWONAKENEE§§,
Pipop LUMYONG§§, Chiradej CHAMSWARNG§§§, Wen-hua TANG#,
Sundar K. SHRESTHA##, Masayasu KATO###, Naoya FUJII**, Seishi AKINO**,
Norio KONDO**, Kiroku KOBAYASHI** and Akira OGOSHI**

Abstract

The mating type, allozyme genotypes of malic enzyme, glucose-6-phosphate isomerase and peptidase loci, and metalaxyl sensitivity of 336 *Phytophthora infestans* isolates collected in Korea, India, Taiwan, Indonesia, Thailand, Nepal, and China between 1992 and 1997 were determined. Only A1 mating type isolates were detected in India and Taiwan, and only A2 isolates in Korea and Indonesia, while both mating type isolates were detected in Thailand, Nepal, and China. The isolates from Korea, India, Taiwan, and Indonesia had a single allozyme genotype respectively, while the isolates from Thailand, Nepal, and China had two or three allozyme genotypes. Isolates that were highly resistant to metalaxyl were found in Korea, Indonesia, and China. All of the isolates from Taiwan and India, and some of the isolates from Thailand, Nepal, and northern and southern areas of China, belonged to the old population of *P. infestans*, which was predominant worldwide until the appearance of A2 isolates outside central Mexico. Some of the isolates from Thailand and Nepal were from new populations that have been discovered since the appearance of A2 isolates outside central Mexico. All of the isolates from Korea and Indonesia and most of the isolates from China belonged to two specific populations, which have been rarely detected elsewhere. The occurrence of these separate populations in Asia suggests that they followed a different migration pathway, or that they are better adapted to Asian conditions than to those elsewhere in the world.

(Received October 16, 1998 ; Accepted December 27, 1998)

Key words : *Phytophthora infestans*, populations, mating type, allozyme genotype, metalaxyl sensitivity, Asian countries.

* This work was supported by grants-in-aid from the Ministry of Education, Science, Sports and Culture of Japan (No. 04041016 ; No. 08041129).

** Laboratory of Plant Pathology, Faculty of Agriculture, Hokkaido University, Sapporo 060-8589, Japan 北海道大学農学部

*** Present address : Aomori Prefectural Agricultural Experiment Station, Sakaimatu, Kuroishi 036-0389, Japan 現在 : 青森県農業試験場

† Department of Agricultural Biology, College of Agriculture, Chonbuk National University, Chonju 561-756, Korea 韓国全北大学

†† Department of Mycology and Plant Pathology, Institute of Agricultural Sciences, Baranas Hindu University, Varanasi-221005, India インドバラナシヒन्दウー大学

††† Taiwan Forestry Research Institute, Botanical Garden, 53 Nan-hai Road, Taipei, Taiwan, Republic of China 中国台湾省林業試験場

‡ Lembang Horticultural Research Institute, P.O. Box 587, Lembang, Bandung, Indonesia インドネシアレンバン園芸研究所

§§ Faculty of Agriculture, Chiang Mai University, Chiang Mai 50002, Thailand タイチェンマイ大学

§§§ Department of Plant Pathology, Kasetsart University, Kamphaen Saen, Nakhon Pathom 73140, Thailand タイカセサート大学

Department of Plant Pathology, China Agricultural University, Beijing 100094, P.R. China 中国農業大学

Plant Pathology Division, Nepal Agricultural Research Council, Khumaltar, Lalitpur, P.O. Box 1126, Kathmandu, Nepal ネパール国立農業研究所

Hokkaido National Agricultural Experiment Station, Sapporo 062-8555, Japan 北海道農業試験場

INTRODUCTION

Phytophthora infestans (Mont.) de Bary is the fungus that causes late blight of potato and tomato around the world. *P. infestans* is heterothallic and has two mating types, A1 and A2. Sexual reproduction and the production of oospores can only occur when isolates of the two mating types cross. Until A2 mating type isolates were discovered in Switzerland¹⁷⁾, it was thought that only A1 type existed outside the central highlands of Mexico, which is generally thought to be the center of origin of *P. infestans*. All of the isolates except those from central Mexico are of a single clonal lineage. Since then, further occurrences of A2 mating type isolates have been discovered outside Mexico^{3-7,9,16,19,20,26,27,31,32,36,37,40)}, and different clones have been found in various locations. It is thought that migration has led to many of the changes seen in *P. infestans* populations worldwide.

Many researchers have studied the characteristics of *P. infestans* populations, relying on various markers, such as mating type, allozyme, metalaxyl sensitivity, virulence, nuclear DNA content, nuclear DNA fingerprinting, and mitochondrial DNA restriction fragment length polymorphism¹¹⁾.

It is generally thought that two major migrations of *P. infestans* have occurred in the world. The first major migration became evident in the 1840's when it caused the Irish potato famine, as well as epidemics in the mid-Atlantic and northeastern regions of the United States¹¹⁾. Most of the populations of this initial global migration were a single clonal lineage that is called the old genotype or old population. After a report of A2 mating type in Western Europe in 1981¹⁷⁾, very variable A2 strains have been discovered in many areas of the world^{3-7,9,16,19,20,26,27,31,32,36,37,40)}. These represent the second major migration, and are called the new genotypes or new populations.

In this study, we examined the mating type, genotype at three allozyme loci, and metalaxyl sensitivity of *P. infestans* isolates. The mating type of heterothallic *P. infestans* is an important characteristic that is readily determined. Since A2 mating type isolates were not detected outside central Mexico prior to the 1980's, mating type is a very useful marker for changes in *P. infestans* populations. Allozymes provided the first unambiguous markers present in sufficient numbers of isolates for reliable genetic studies of *P. infestans*³⁸⁾. Changes in population allozyme genotypes suggest that sexual recombination or migrations of new clonal lineages have occurred. Metalaxyl is a systemic fungicide used to control late blight, and therefore, from an agricultural perspective, it is important to assay metalaxyl sensitivity.

Investigation of different populations' characteristics, diversity, and geographical relationships should tell us more about possible population migrations and the occurrence of sexual recombination in the field.

Although there have been many reports on the distribution of *P. infestans* populations in Europe^{1,5,10,29,35,37,40)}, the United States^{13,15,21)}, and Central¹⁴⁾ and South America^{8,11,39)}, there have been few reports on populations in Asia^{18,19,22-25)}.

We had three objectives in this study. The first was to clarify the distribution of *P. infestans* populations in the seven Asian countries studied (Korea, India, Taiwan, Indonesia, Thailand, Nepal, and China). The second was

Table 1. Sources of *Phytophthora infestans* isolates

Country Location	Number of sites	Year of collection	Host	Sample size
Korea				
Chonbuk	6	1992	Potato	12
Chungnam	2	1992	Potato	3
Kangwon	1	1992	Potato	1
India				
Allahabad	2	1993	Potato	4
Varanasi	2	1993	Potato	4
Ghazipur	3	1993	Potato	4
Taiwan				
Puli	2	1993	Tomato	6
Sini	6	1993	Tomato	19
Kosing	2	1993	Tomato	2
Hualian	1	1993	Tomato	1
Ilan	3	1993	Tomato	14
Indonesia				
NK ^{a)}	4	1993	Potato	4
Thailand				
Chiang Mai	17	1994	Potato	37
	7	1994	Tomato	18
Nepal				
Kathmandu	8	1996	Potato	24
	5	1996	Tomato	15
Nepalganj	1	1996	Potato	4
Pokhara	1	1996	Potato	4
Nigale	1	1996	Potato	3
Kathmandu	1	1997	Potato	1
	1	1997	Tomato	6
Shakhu	1	1997	Potato	1
Panuti	1	1997	Potato	2
Lumle	1	1997	Potato	7
Jiri	1	1997	Potato	2
Nigale	1	1997	Potato	1
Panchkhel	1	1997	Potato	1
Jasbire	1	1997	Potato	8
Rakshe	1	1997	Potato	6
Pasupatinagar	1	1997	Potato	7
Manebhanjag	1	1997	Potato	6
China				
Wei Chang (the northern part)	8	1996	Potato	41
Lanzhou(the cen- tral inland part)	9	1996	Potato	52
Kunming (the southern part)	3	1997	Potato	14
Chengdu (the southern part)	1	1997	Tomato	2

a) NK=Not known.

to compare the characteristics of Asian populations with the characteristics of those elsewhere, and investigate the relationships between them. The final objective was to study the question of migration and examine migration pathways.

MATERIALS AND METHODS

Sources of isolates The sources and origins of the isolates studied are shown in Table 1 and Fig. 1. A total of 336 isolates was collected in seven Asian countries between 1992 and 1997. Japanese, U.K., and Mexican isolates were used as controls. All of the isolates collected in Korea, India, and Indonesia were from potatoes, while those collected in Taiwan were from tomatoes. Isolates from Thailand, China, and Nepal were collected from both potatoes and tomatoes. Since China covers a very large area, three areas were distinguished: the northern (Wei Chang), central inland (Lanzhou), and southern (Kunming and Chengdu) areas.

Samples were taken from infected potato or tomato tissue (foliage or tubers). A single lesion from a leaf or infected tuber was placed on rye B agar medium²⁾ containing ampicillin sodium (200 ppm), nystatin (100 ppm), and rifampicin (50 ppm). Subsequently, sporangia that formed on the rye B agar medium were transferred to rye A agar medium²⁾ containing the same antibiotics.

Once colonies of *P. infestans* were established, the isolates were maintained on slants of rye A agar at 18°C in the dark.

Mating type Mating type was determined by pairing each isolate with known A1 and A2 tester isolates of *P. infestans* on 10% clarified V8 juice agar medium. After 7 to 10 days of incubation at 20°C in the dark, the presence or absence of oospores was observed. Isolates that formed oospores with the A1 tester but not with the A2 were designated A2, and vice versa. All pairings were repeated twice.

Allozyme analysis Cultures for allozyme analysis were grown in pea broth medium for 10 to 14 days at 20°C. Mycelia were harvested by vacuum filtration, frozen with liquid nitrogen, and ground with a mortar and pestle. Subsequently, Tris-citrate buffer (0.009 M trizma base, 0.003 M citric acid, pH 7.0)³⁰⁾ was added to the ground mycelia to make an homogenate, which was centrifuged at 23,000×*g* for 20 min. After centrifugation, the supernatant was used as the extracted protein sample.

The genotype of all the isolates was determined at three allozyme loci: malic enzyme (*Me*; EC1.1.1.40), glucose-6-phosphate isomerase (*Gpi*; EC5.3.1.9), and peptidase (*Pep*; EC3.4.3.1). For electrophoresis, 12% starch gels were used. Starch gel electrophoresis was carried out using the standard buffer systems described

Fig. 1. Asian locations where the isolates of *Phytophthora infestans* used in this study were collected. The sample sites are numbered. 1, Chonbuk; 2, Chungnam; 3, Kangwon; 4, Allahabad; 5, Varanasi; 6, Ghazipur; 7, Puli, Sini, Kosing; 8, Hualian; 9, Ilan; 10, Jakarta; 11, Chiang Mai; 12, Kathmandu, Shakhu, Panuti; 13, Nepalganj, Pokhara, Lumle; 14, Nigale, Jiri, Panchkhel; 15, Jasbire, Rakshe, Pasupatinagar, Manebhanjag; 16, Wei Chang; 17, Lanzhou; 18, Kunming; 19, Chengdu.

by Mosa *et al.*²⁴⁾. The staining procedures were adapted after Selander *et al.*²⁸⁾. Standards scored by Mosa *et al.* were used as controls to determine the identity of allozyme alleles. All of the isolates were analyzed two or three times.

Metalaxyl sensitivity The metalaxyl sensitivity of the isolates was determined by the hyphal growth on rye A agar medium with added metalaxyl (0, 0.1, 1, 10 and 100 ppm). The inocula consisted of 5 mm diameter plugs taken from the edge of colonies on rye A agar medium that were about 7 days old. Four inocula of each isolate were placed equidistant from each other on the agar plate. The cultures were incubated for 7 days at 20°C in the dark. After 7 days, hyphal growth was measured and metalaxyl sensitivity was determined. Isolates with a metalaxyl ED₅₀ concentration of less than 0.1 ppm were deemed sensitive and those with a concentration of equal to or more than 0.1 ppm were deemed resistant.

RESULTS

Mating type

The mating types of the isolates are shown in Tables 2 and 5. All of the isolates collected in India and Taiwan were A1 mating type, and all of the isolates collected in Korea and Indonesia were A2 mating type. Isolates of both mating types were found in samples from Thailand, China, and Nepal. Of 55 isolates from Thailand, 23 were A1 mating type and 32 were A2. Of 98 isolates from Nepal, 64 were A1 and 34 were A2. All 41 isolates from northern China were A1 mating type, 51 of 52 isolates from central inland China were A1, with only one A2 mating type, and 10 of the 16 isolates from southern China were A1 and 6 were A2 mating type.

All of the isolates from tomatoes were A1 mating type.

Allozyme genotype

The allozyme genotypes of the *Me*, *Gpi*, and *Pep* loci

Table 2. Mating types of *Phytophthora infestans* isolates studied

Country	Number of isolates	
	A1 mating type	A2 mating type
Korea	0	16
India	12	0
Taiwan	42	0
Indonesia	0	4
Thailand	23	32
Nepal	64	34
China		
the northern part	41	0
(Wei Chang)		
the central inland part	51	1
(Lanzhou)		
the southern part	10	6
(Kunming, Chengdu)		

were determined (Tables 3 and 5). The genotypes in this section are given in the order *Me*, *Gpi*, and *Pep*. All of the isolates from Korea and Indonesia were 90/100, 100/100, and 96/96. All of the isolates from India were 100/100, 100/100, and 92/100. All of the isolates from Taiwan were 100/100, 86/100, and 92/100. Of 55 isolates from Thailand, 23 were 100/100, 86/100, and 92/100, and 32 were 100/100 for all three allozyme loci. Of 98 isolates from Nepal, 46 were 100/100, 86/100, and 92/100, 18 were 100/100, 100/100, and 92/100, and 34 were 100/100 for all three allozyme loci. Most of the Chinese isolates had a unique allozyme locus for *Gpi*, and its mobility was scored 98/98. Of 41 isolates from northern China, only one was 100/100, 86/100, and 92/100, and the rest were 90/

Table 3. Allozyme genotypes of *Phytophthora infestans* isolates studied

Country	Number of isolates	Allozyme genotype ^{a)}		
		<i>Me</i>	<i>Gpi</i>	<i>Pep</i>
Korea	16	90/100	100/100	96/96
India	12	100/100	100/100	92/100
Taiwan	42	100/100	86/100	92/100
Indonesia	4	90/100	100/100	96/96
Thailand	23	100/100	86/100	92/100
	32	100/100	100/100	100/100
Nepal	46	100/100	86/100	92/100
	18	100/100	100/100	92/100
	34	100/100	100/100	100/100
China				
the northern part	1	100/100	86/100	92/100
	40	90/100	98/98	100/100
the central inland part	43	100/100	98/98	100/100
	9	90/100	98/98	100/100
the southern part	2	100/100	86/100	92/100
	14	100/100	98/98	100/100

a) *Me* = Malic enzyme, *Gpi* = Glucosephosphate isomerase, *Pep* = Peptidase.

Table 4. Degree of resistance to metalaxyl among *Phytophthora infestans* isolates studied

Country	Number of isolates	ED ₅₀ (ppm) ^{a)}				
		<0.1	0.1 ≤	1 ≤	10 ≤	100 ≤
Korea	16	1	0	0	11	4
India	12	12	0	0	0	0
Taiwan	42	39	3	0	0	0
Indonesia	4	0	0	0	2	2
Thailand	55	55	0	0	0	0
Nepal	98	98	0	0	0	0
China						
the northern part	41	30	0	0	3	8
the central inland part	52	51	1	0	0	0
the southern part	16	16	0	0	0	0

a) ED₅₀ is the dose of fungicide that inhibits 50% of mycelial growth. Classes of responses were determined on the basis that ED₅₀ less than 0.1 ppm was sensitive, and equal to or more than 0.1 ppm was resistant.

Table 5. Characteristics of *Phytophthora infestans* isolates studied

Country	Mating type	Allozyme genotype ^{a)}			Response to metalaxyl	Host	Sample size
		<i>Me</i>	<i>Gpi</i>	<i>Pep</i>			
Korea	A2	90/100	100/100	96/96	Sensitive	Potato	1
	A2	90/100	100/100	96/96	Resistant	Potato	15
India	A1	100/100	100/100	92/100	Sensitive	Potato	12
Taiwan	A1	100/100	86/100	92/100	Sensitive	Tomato	39
	A1	100/100	86/100	92/100	Resistant ^{b)}	Tomato	3
Indonesia	A2	90/100	100/100	96/96	Resistant	Potato	4
Thailand	A1	100/100	86/100	92/100	Sensitive	Potato	5
	A1	100/100	86/100	92/100	Sensitive	Tomato	18
Nepal	A2	100/100	100/100	100/100	Sensitive	Potato	32
	A1	100/100	86/100	92/100	Sensitive	Potato	25
	A1	100/100	86/100	92/100	Sensitive	Tomato	21
	A1	100/100	100/100	92/100	Sensitive	Potato	18
	A2	100/100	100/100	100/100	Sensitive	Potato	34
China							
the northern part	A1	100/100	86/100	92/100	Sensitive	Potato	1
	A1	90/100	98/98	100/100	Sensitive	Potato	29
	A1	90/100	98/98	100/100	Resistant	Potato	11
the central inland part	A1	100/100	98/98	100/100	Sensitive	Potato	41
	A1	100/100	98/98	100/100	Resistant ^{b)}	Potato	1
	A1	90/100	98/98	100/100	Sensitive	Potato	9
the southern part	A2	100/100	98/98	100/100	Sensitive	Potato	1
	A1	100/100	86/100	92/100	Sensitive	Tomato	2
	A1	100/100	98/98	100/100	Sensitive	Potato	8
	A2	100/100	98/98	100/100	Sensitive	Potato	6

a) *Me* : Malic enzyme, *Gpi* : Glucosephosphate isomerase, *Pep* : Peptidase.

b) Metalaxyl sensitivity of four isolates was low level resistant.

100, 98/98, and 100/100. Of 52 isolates from central inland China, 43 were 100/100, 98/98, and 100/100, and 9 were 90/100, 98/98, and 100/100. Of 16 isolates from southern China, two were 100/100, 86/100, and 92/100, and 14 were 100/100, 98/98, and 100/100.

All of the isolates from tomatoes were 100/100, 86/100, and 92/100.

Metalaxyl sensitivity

The metalaxyl sensitivity of the isolates is shown in Tables 4 and 5. All of the isolates collected in India, Thailand, Nepal, and southern China were sensitive to metalaxyl. On the other hand, all but one of the isolates collected in Korea was resistant to metalaxyl, and all of the isolates collected in Indonesia were resistant. Most of the isolates collected in Taiwan and central inland China were sensitive, but three of the former and one of the latter showed some resistance (intermediate). Of 41 isolates collected in northern China, 30 were sensitive and 11 were resistant.

All of the isolates from tomatoes were sensitive to metalaxyl.

DISCUSSION

The first major migration of *P. infestans* became evident in the 1840's when it caused the Irish potato famine, as well as epidemics in the mid-Atlantic and northeastern regions of the United States¹¹⁾. These out-

breaks probably resulted from transportation of the fungus from the central highlands of Mexico, generally thought to be its center of origin, to the United States and Europe. Most of the populations of this initial global migration were a single clonal lineage that is called the old genotype or old population (A1, 86/100 for *Gpi* and 92/100 for *Pep*). Until the A2 mating type was reported in Western Europe in 1981¹⁷⁾, it was thought that only the old population existed outside central Mexico. The old population is designated US-1, and its strains are identified by their mating type, the presence or absence of seven *Gpi* and five *Pep* alleles, and the presence or absence of a band at each of 25 DNA fingerprint loci¹³⁾. Subsequently, very variable A2 strains have been discovered in many areas of the world^{3-7,9,16,19,20,26,27,31,32,36,37,40)}. These populations of the second major migration are called the new genotypes or new populations.

In our study, the mating type, genotype at three allozyme loci, and metalaxyl sensitivity of *P. infestans* isolates from seven Asian countries were determined (Tables 2-5). DNA fingerprinting has not yet been done. All of the isolates from Taiwan, 23 of 55 isolates from Thailand, 46 of 98 isolates from Nepal, 1 isolate from northern China, and 2 of 16 isolates from southern China were of the old population (A1, 86/100 for *Gpi* and 92/100 for *Pep*) that was predominant worldwide until recently. All of the isolates from India and 18 of the 98 isolates from Nepal were another strain of the old

population (A1, 100/100 for *Gpi* and 92/100 for *Pep*). This second genotype has also been detected occasionally in the United States^{13,34} where it was first found outside central Mexico. Thirty-two of 55 isolates from Thailand and 34 of 98 isolates from Nepal belonged to the new population (A2, 100/100 for *Gpi* and 100/100 for *Pep*), which has been detected in the United States, Canada, the Netherlands, Poland, Germany, Israel, and Japan^{12,33} since the appearance of A2 isolates outside central Mexico. These old and new populations probably migrated from central Mexico to the United States and Europe, and then to Asia.

All of the isolates from Korea and Indonesia were from the specific population (A2, 100/100 for *Gpi* and 96/96 for *Pep*). Identical isolates have also been found in Poland³⁵ and Japan²⁴. Koh *et al.*¹⁹ reported the same results for the Korean isolates. Since this population has not been detected elsewhere, it may have followed a unique migration pathway. Most of the Chinese isolates were also from the specific population (A1 or A2, 98/98 for *Gpi* and 100/100 for *Pep*). This phenotype has only been detected in central Mexico and not in other Asian countries. This may also represent a unique migration pathway or a mutation after migration. It is possible that these specific populations of *P. infestans* migrated directly from central Mexico to Asia, or that these populations are not well suited to conditions in the United States and Europe, but are well adapted to Asia.

It is interesting that most of metalaxyl-resistant isolates were collected from Korea, Indonesia, and northern China, and these isolates have the specific genotype of allozyme loci. The relationship between metalaxyl resistance and specific genotype must be studied.

All of the isolates from tomatoes in this study were A1, allozyme genotype 100/100 for *Me*, 86/100 for *Gpi*, and 92/100 for *Pep*, and sensitive to metalaxyl.

Both mating type isolates were detected at a few sampling sites in Thailand, Nepal, and China. Although it is possible that sexual reproduction occurs in these locations, it has not been demonstrated. The diversity of *P. infestans* populations in Asian countries is not very high at present, because sexual reproduction may occur rarely. If newer strains (populations) of the fungus migrate to Asia and sexual recombinants form, the genetic diversity of *P. infestans* increases, and then the control of late blight of potato and the management of potato production may become more difficult. In order to investigate the population dynamics of the fungus, populations in the same sites must be monitored for several years.

We thank Dr. R.C. Shattock for providing U.K. isolates, and also Dr. M. Coffey for providing Mexican isolates. We thank Dr. N. Sato for his generous cooperation in collecting and obtaining Japanese isolates.

Literature cited

1. Andrivon, D., Béasse, C. and Laurent, C. (1994). Characterization of isolates of *Phytophthora infestans* collected in northwestern France from 1988 to 1992. *Plant Pathol.* 43: 471-478.
2. Caten, C.E. and Jinks, J.L. (1968). Spontaneous variability of single isolates of *Phytophthora infestans*. I. Cultural variation. *Can. J. Bot.* 46: 329-348.
3. Cooke, L.R., Currie, T.S. and Penney, R.E. (1993). The mating type of *Phytophthora infestans* in Northern Ireland. *Phytophthora Newsletter* 19: 4-5.
4. Cooke, L.R., Swan, R.E. and Currie, T.S. (1995). Incidence of the A2 mating type of *Phytophthora infestans* on potato crops in Northern Ireland. *Potato Res.* 38: 23-29.
5. Daggett, S.S., Götz, E. and Therrien, C.D. (1993). Phenotypic changes in population of *Phytophthora infestans* from eastern Germany. *Phytopathology* 83: 319-323.
6. Deahl, K.L., Goth, R.W., Young, R., Sinden, S.L. and Gallegly, M.E. (1991). Occurrence of the A2 mating type of *Phytophthora infestans* in the United States and Canada. *Am. Potato J.* 68: 717-725.
7. El-Korany, A.E., Shaw, D.S. and Abdel-Sattar, M.A. (1990). *Phytophthora infestans* in Egypt. *Phytophthora Newsletter* 16: 41-42.
8. Forbes, G.A., Escobar, X.C., Ayala, C.C., Revelo, J., Ordonez, M.E., Fry, B.A., Doucett, K. and Fry, W.E. (1997). Population genetic structure of *Phytophthora infestans* in Ecuador. *Phytopathology* 87: 375-380.
9. Frinking, H.D., Davidse, L.C. and Limburg, H. (1987). Oospore formation by *Phytophthora infestans* in host tissue after inoculation with isolates of opposite mating type found in the Netherlands. *Neth. J. Plant Pathol.* 93: 147-149.
10. Fry, W.E., Drenth, A., Spielman, L.J., Mantel, B.C., Davidse, L.C. and Goodwin, S.B. (1991). Population genetic structure of *Phytophthora infestans* in the Netherlands. *Phytopathology* 81: 1330-1336.
11. Fry, W.E., Goodwin, S.B., Dyer, A.T., Matuszak, J.M., Drenth, A., Tooley, P.W., Sujkowski, L.S., Koh, Y.J., Cohen, B.A., Spielman, L.J., Deahl, K.L., Inglis, D.A. and Sandlan, K.P. (1993). Historical and recent migrations of *Phytophthora infestans*: chronology, pathways, and implications. *Plant Dis.* 77: 653-661.
12. Fry, W.E. and Spielman, L.J. (1991). Population biology of *Phytophthora infestans*: *Phytophthora infestans*, the cause of late blight of potato. In *Advances in Plant Pathology*, Vol. 7 (Ingram, D.S. and Williams, P.H. eds.), Academic Press, London, pp. 171-192.
13. Goodwin, S.B., Cohen, B.A., Deahl, K.L. and Fry, W.E. (1994). Migration from northern Mexico as the probable cause of recent genetic changes in populations of *Phytophthora infestans* in the United States and Canada. *Phytopathology* 84: 553-558.
14. Goodwin, S.B., Spielman, L.J., Matuszak, J.M., Bergeron, S.N. and Fry, W.E. (1992). Clonal diversity and genetic differentiation of *Phytophthora infestans* populations in northern and central Mexico. *Phytopathology* 82: 955-961.

15. Goodwin, S.B., Sujkowski, L.S., Dyer, A.T., Fry, B.A. and Fry, W.E. (1995). Direct detection of gene flow and probable sexual reproduction of *Phytophthora infestans* in northern North America. *Phytopathology* 85: 473-479.
16. Hermansen, A. and Amundsen, T. (1995). Mating types of *Phytophthora infestans* in Norway. In *Phytophthora infestans* 150 (Dowley, L.J., Bannon, E., Cooke, L.R., Keane, T. and O'Sullivan, E. eds.), Boole Press, Dublin, Ireland, pp. 77-82.
17. Hohl, H.R. and Iselin, K. (1984). Strains of *Phytophthora infestans* from Switzerland with A2 mating type behavior. *Trans. Br. mycol. Soc.* 83: 529-530.
18. Kato, M., Sato, N., Takahashi, K. and Shimanuki, T. (1998). Yearly change of frequency and geographical distribution of A2 mating type isolates of *Phytophthora infestans* in Japan from 1987 to 1993. *Ann. Phytopathol. Soc. Jpn.* 64: 168-174.
19. Koh, Y.J., Goodwin, S.B., Dyer, A.T., Cohen, B.A., Ogoshi, A., Sato, N. and Fry, W.E. (1994). Migrations and displacements of *Phytophthora infestans* populations in east Asian countries. *Phytopathology* 84: 922-927.
20. Malcolmson, J.F. (1985). *Phytophthora infestans* A2 compatibility type recorded in Great Britain. *Trans. Br. mycol. Soc.* 85: 531.
21. Miller, J.S., Hamm, P.B. and Johnson, D.A. (1997). Characterization of the *Phytophthora infestans* population in the Columbia Basin of Oregon and Washington from 1992 to 1995. *Phytopathology* 87: 656-660.
22. Mosa, A.A. (1992). Studies on the population of *Phytophthora infestans*, the cause of potato late blight in Japan. Thesis of Hokkaido University, Sapporo, Japan.
23. Mosa, A.A., Kato, M., Sato, N., Kobayashi, K. and Ogoshi, A. (1989). Occurrence of the A2 mating type of *Phytophthora infestans* on potato in Japan. *Ann. Phytopathol. Soc. Jpn.* 55: 615-620.
24. Mosa, A.A., Kobayashi, K., Ogoshi, A., Kato, M. and Sato, N. (1993). Isoenzyme polymorphism and segregation in isolates of *Phytophthora infestans* from Japan. *Plant Pathol.* 42: 26-34.
25. Ogoshi, A., Kobayashi, K., Mosa, A.A. and Sato, N. (1988). Compatibility types of *Phytophthora infestans* in Hokkaido. The 5th International Congress of Plant Pathology, Kyoto, Japan, p. 182.
26. Ritch, D.L., Spielman, L.J., Sujkowski, L.S. and Therrien, C.D. (1990). The nuclear DNA content, mating type and metalaxyl sensitivity of fifty-three isolates of *Phytophthora infestans* from Poland. *Phytopathology* 80: 123 (Abstr.).
27. Ritch, D.L., Therrien, C.D., Daggett, S.S., Sim, J.H. and Sujkowski, L.S. (1991). *Phytophthora infestans* in Poland from 1987-1989, nuclear DNA content, mating type and response to metalaxyl. *Phytopathology* 81: 1190 (Abstr.).
28. Selander, R.K., Caugant, D.A., Ochman, H., Musser, J.M., Gilmour, K.N. and Whittam, T.S. (1986). Methods of multilocus enzyme electrophoresis for bacterial population genetics and systematics. *Appl. Environ. Microbiol.* 51: 873-884.
29. Shattock, R.C., Shaw, D.S., Fyfe, A.M., Dunn, J.R., Loney, K.H. and Shattock, J.A. (1990). Phenotypes of *Phytophthora infestans* collected in England and Wales from 1985 to 1988: mating type, response to metalaxyl and isoenzyme analysis. *Plant Pathol.* 39: 242-248.
30. Shaw, C.R. and Prasad, R. (1970). Starch gel electrophoresis of enzymes—A compilation of recipes. *Biochem. Genet.* 4: 297-320.
31. Shaw, D.S., Fyfe, A.M., Hibberd, P.G. and Abdel-Sattar, M.A. (1985). Occurrence of the rare A2 mating type of *Phytophthora infestans* on imported Egyptian potatoes and the production of sexual progeny with A1 mating types from the UK. *Plant Pathol.* 34: 552-556.
32. Singh, B.P., Roy, S., Bhattacharyya, S.K. and Shekawat, G.S. (1993). Occurrence of A2 mating type of *Phytophthora infestans* in India. *Phytophthora Newsletter* 19: 6-7.
33. Spielman, L.J. (1991). Isozymes and the population genetics of *Phytophthora infestans*. In *Phytophthora* (Lucas, J.A., Shattock, R.C., Shaw, D.S. and Cooke, L.R. eds.), Cambridge University Press, Cambridge, pp. 231-241.
34. Spielman, L.J., Drenth, A., Davidse, L.C., Sujkowski, L.J., Gu, W., Tooley, P.W. and Fry, W.E. (1991). A second world-wide migration and population displacement of *Phytophthora infestans*? *Plant Pathol.* 40: 422-430.
35. Sujkowski, L.S., Goodwin, S.B., Dyer, A.T. and Fry, W.E. (1994). Increased genotypic diversity via migration and possible occurrence of sexual reproduction of *Phytophthora infestans* in Poland. *Phytopathology* 84: 201-207.
36. Tantius, P.H., Fyfe, A.M., Shaw, D.S. and Shattock, R.C. (1986). Occurrence of the A2 mating type and self-fertile isolates of *Phytophthora infestans* in England and Wales. *Plant Pathol.* 35: 578-581.
37. Therrien, C.D., Ritch, D.L., Davidse, L.C., Jespers, A.D.B.K. and Spielman, L.J. (1989). Nuclear DNA content, mating type and metalaxyl sensitivity of eighty-three isolates of *Phytophthora infestans* from the Netherlands. *Mycol. Res.* 92: 140-146.
38. Tooley, P.W., Fry, W.E. and Villarreal Gonzales, M.J. (1985). Isozyme characterization of sexual and asexual *Phytophthora infestans* populations. *J. Hered.* 76: 431-435.
39. Tooley, P.W., Therrien, C.D. and Ritch, D.L. (1989). Mating type, race composition, nuclear DNA content, and isozyme analysis of Peruvian isolates of *Phytophthora infestans*. *Phytopathology* 79: 478-481.
40. Tooley, P.W., Therrien, C.D., Sim, J.H., O'Sullivan, E. and Dowley, L.J. (1993). Mating type, nuclear DNA content and isozyme genotypes of Irish isolates of *Phytophthora infestans*. *Mycol. Res.* 97: 1131-1134.

和 文 摘 要

西村 亮・佐藤香緒理・Wang Hyu LEE・U.P. SINGH・Tun-tschu CHANG・Euis SURYANINGSIH・Somkiat SUWONAKENEE・Pipop LUMYONG・Chiradej CHAMSWARNG・Wen-hua TANG・Sundar K. SHRESTHA・加藤雅康・藤井直哉・秋野聖之・近藤則夫・小林喜六・生越 明：アジア7カ国における *Phytophthora infestans* の個体群分布

1992年から1997年の間に韓国, インド, 台湾, インドネシア,

タイ、ネパール、中国から採集した *Phytophthora infestans* 336 菌株について交配型、アイソザイム(リンゴ酸酵素, グルコースホスヘートイソメラーゼ, ペプチダーゼ)の遺伝子型, メタラキシル感受性を調べた。インドと台湾からは A1 菌株のみが, 韓国とインドネシアからは A2 菌株のみが検出されたが, タイ, ネパール, 中国からは両交配型菌株とも検出された。韓国, インド, 台湾, インドネシアの菌株はそれぞれ単型のアイソザイムの遺伝子型であったが, タイ, ネパール, 中国の菌株は 2 つもしくは 3 つの遺伝子型を示した。韓国, インドネシア, 中国にはメタラキシルに強い耐性を持つ菌株があった。台湾, インドのすべて,

およびタイ, ネパール, 中国北部, 南部の一部の菌株は, 中央メキシコ以外での A2 菌株出現以前に世界中で優占的であった古いタイプの個体群であった。タイとネパールの一部の菌株は, 中央メキシコ以外での A2 菌株出現以降に発見された新しいタイプの個体群であった。韓国とインドネシアのすべて, および中国の大部分の菌株は, 他地域ではほとんどみられない特異的な個体群であった。アジアにおいてこれらの異なる個体群の存在は, 移入経路が様々であったこと, もしくはそれら個体群が世界の他地域に比べて, アジアの環境により適応できたことを示唆している。