

# Molecular analysis of repeated DNA sequences from the rice blast fungus *Magnaporthe grisea*

P. Kachroo, S.A. Leong, and B.B. Chattoo

Genome organization and distribution of repeated DNA sequences were studied in the rice blast fungus *Magnaporthe grisea*. The analysis led to the identification of an inverted repeat transposon and a short interspersed nuclear element. Both of these elements were isolated as insertions into unrelated repeated DNA sequences, a process that appears to be of common occurrence in the genome of *M. grisea*. The repeated DNA sequences were characterized with respect to their fingerprinting patterns in rice and nonrice isolates of *M. grisea*, dispersion in the genome, copy number, and sequence characteristics. The close physical association of diverse repeated DNA sequences and the genome rearrangements caused by them indicate that they may also contribute to genome variability seen among isolates of *M. grisea*.

Rice blast, caused by the filamentous ascomycete *Magnaporthe grisea*, is one of the most devastating diseases of cultivated rice. This pathogen is classified into various pathotypes or races based on the infection pattern obtained on a set of differential rice cultivars and, like most other phytopathogenic fungi, shows a high level of variability (Latterell 1975). The variable nature of the pathogen often leads to breakdown of host resistance leading to widespread epidemics. Thus, breeding for durable blast resistance is one of the major challenges faced by rice breeders (Ou 1985).

Various models and hypotheses have been proposed to explain the genetic variability among isolates of *M. grisea* (Yamasaki and Niizeki 1965, Giatgong and Frederiksen 1969, Ou 1985). However, an understanding of this phenomenon at a molecular level is still lacking. We have initiated an analysis of the genomic architecture of this fungus in an attempt to study the basis of variability. As a first step, we began an analysis of repeated DNA sequences with respect to their genome organization, since these sequences have been demonstrated to mediate DNA rearrangements in a variety of organisms (Fedoroff 1979, Petes 1980, Coen et al 1982, Rothstein et al

1987). Here, we report on a detailed analysis of three different repetitive elements from *M. grisea* and demonstrate how these may mediate genomic rearrangements in this fungus.

## Results and discussion

A repeat element of 1.3 kb was cloned from the genome of *M. grisea* and studied with respect to its fingerprinting pattern among rice and nonrice isolates. Southern hybridization analysis of genomic DNA from 36 isolates representing different geographical regions, when digested with *Pst*I and probed with a 1.3-kb repeat, showed an intense band at 1.3 kb and several higher molecular weight bands (Fig. 1). The repeat was present at a high copy number (approximately 100) in both the subgroups of *M. grisea*. Contour-clamped homogeneous electric field (CHEF) analysis carried out with both rice and nonrice isolates showed that the repeat was dispersed in nature and was also present on B chromosomes (Fig. 2).

Several members of this repeat family were cloned and found to have heterogeneity in their restriction maps. Spot sequence analysis also showed heterogeneity at the sequence level, which was due to point mutations, transitions, and transversions. The heterogeneity and the presence of several higher molecular weight bands in a Southern blot containing the genomic DNA digested with *Pst*I and probed with the 1.3-kb repeat were indicative of this repeat being prone to genome rearrangements. This hypothesis was investigated by cloning and characterization of 5.1- and 3.2-kb *Pst*I fragments from isolates B101 and B157, respectively.

### Analysis of the 5.1-kb repeat

Restriction mapping and Southern analysis of the 5.1-kb fragment showed that it contained at least two other repeated DNA sequences in addition to the 1.3-kb element. These flanked the 1.3-kb region (Fig. 3a) and also showed a different fingerprinting pattern. Sequence analysis of the 5.1-kb fragment revealed that the 1.3-kb repeat was truncated at the 5' end by 395 bp and that the *Pst*I site, which marked the end of 1.3-kb repeat, had undergone a point mutation resulting in the loss of the site. Sequence analysis of the 2.7-kb region (designated as Mg-RT; Fig. 3a) upstream of the 1.3-kb repeat showed features typical of retroelements that include the presence of TG at the insertion site, 4-bp inverted repeats that mark the start and end of the long terminal repeat (LTR), and homology to the gag and pol regions. It is, therefore, likely that an insertion element, represented by a partial length of 2.7 kb in the 5.1-kb fragment, had inserted within the 1.3-kb repeat, thereby displacing the 395 bp at the 5' end.

The 1.4-kb region downstream of the 3'-*Pst*I site of the 1.3-kb repeat had a DNA fingerprint similar to that of the 1.3-kb repeat and showed an intense band at 1.4 kb in the genomic digests and 4-12 higher molecular weight bands. A similar intensity/pattern of the hybridization signal obtained with 1.3- and 1.4-kb repeat probes and their association in the 5.1-kb *Pst*I fragment prompted us to analyze if the presence of the two elements in the 5.1 kb was a chance occurrence or whether they were parts of a larger repeat element. Southern analysis of genomic DNA digested with 27 restriction

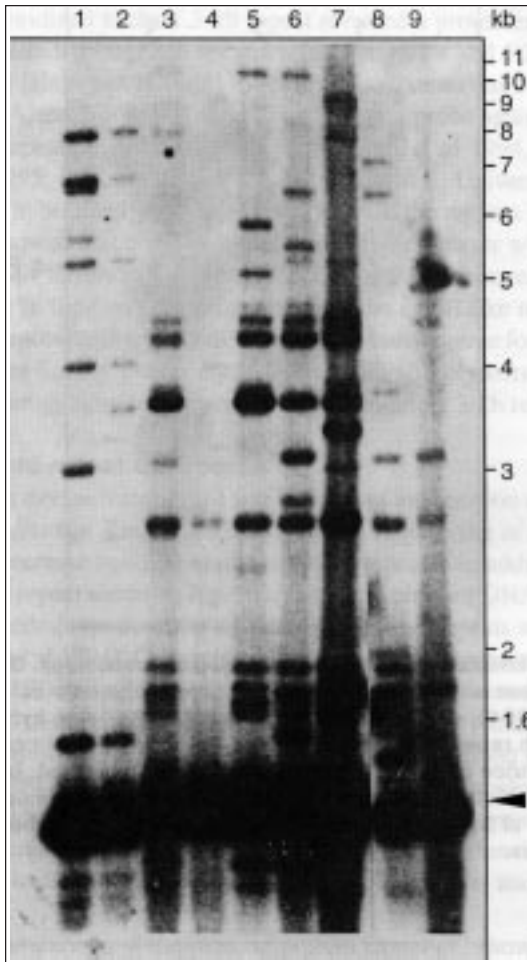


Fig. 1. Southern hybridization of genomic DNA of rice and nonrice pathogens of *M. grisea* probed with a 1.3-kb *Pst*I repeat element. Genomic DNA (2 g) was digested with *Pst*I, electrophoresed through a 0.8% agarose gel, transferred to a nylon membrane, and hybridized with radiolabeled pBC157.3 (1.3-kb *Pst*I fragment from isolate B157 cloned into vector pUC19). The lanes contain DNA from Pr342 (nonrice pathogen, Philippines), lane 1; Pr886 (nonrice pathogen, Philippines), lane 2; Lc454 (nonrice pathogen, Philippines), lane 3; Pg 3393 (nonrice pathogen, India), lane 4; Cb334 (nonrice pathogen, Philippines), lane 5; Ec552 (nonrice pathogen, Philippines), lane 6; Ei476 (nonrice pathogen, Philippines), lane 7; 91-A-58 (rice pathogen, USA), lane 8; 4360-17-1 (rice pathogen, USA), lane 9. The conserved 1.3-kb band is marked by an arrowhead.

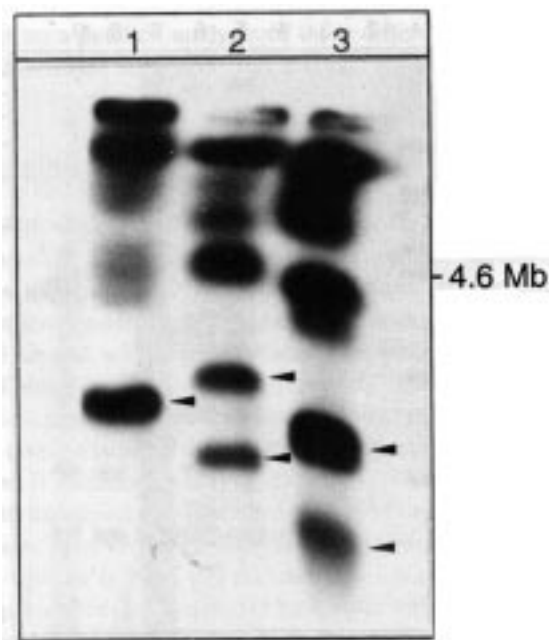


Fig. 2. Southern hybridization analysis of *M. grisea* chromosomes. Chromosome-sized DNA molecules were separated by CHEF-gel electrophoresis as described earlier (Kachroo et al 1994), blotted onto nylon membrane, and hybridized with the radiolabeled 1.3-kb repeat (pBC157.3) probe. The lanes contain chromosomal DNA from isolate A (nonrice pathogen), lane 1; B157 (rice pathogen), lane 2; B101 (rice pathogen), lane 3. Molecular size 4.6 Mb corresponds to chromosome 6 of isolate Guy11 (Skinner et al 1993). Arrowheads show hybridization of the 1.3-kb repeat to the B chromosomes.

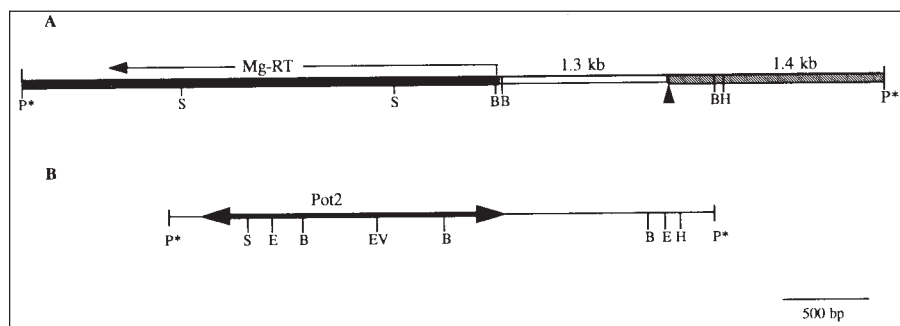


Fig. 3. Restriction map of 5.1-kb (A) and 3.2-kb (B) derivatives of the 1.3-kb *PstI* repeat element. Arrowhead in A denotes the 3' *PstI* site of 1.3 kb, which is lost due to a point mutation. Mg-RT in 5.1 kb is a partial length clone. Triangles in B represent the inverted repeats of Pot2. Restriction sites shown are P, *PstI*; B, *BamHI*; S, *Sall*; E, *EcoRI*; EV, *EcoRV*; H, *HindIII*. Asterisks denote the cloning site in vector pUC19.

enzymes and hybridized to the 1.3-kb repeat revealed a prominent 2-kb *Bam*HI and two less intense *Hind*III fragments of molecular weights 4 and 5.2 kb. Since both 1.3 kb and MGR583 (Hamer et al 1989) hybridized to a conserved 2-kb *Bam*HI band in the genomic DNA, the 1.3/1.4-kb repeat was used as a probe against MGR as well as other available repeats (Skinner et al 1993, Kachroo et al 1994, Leong et al 1994, Kachroo et al 1995; P. Kachroo and B.B. Chattoo, M.S. University, India, unpubl. data). The probe hybridized strongly to MGR583 and the regions showing homology were further narrowed down to 1.3- and 1.4-kb *Pst*I fragments within the MGR583. Our recent analysis has shown that both the 1.3- and 1.4-kb repeats are present as a contiguous piece in the genome and are parts of the LINE-like region of MGR583. Since LINE sequences require the activity of reverse transcriptase for their retroposition, which has a lower fidelity rate as compared with DNA polymerase, it also explains the sequence heterogeneity seen among members of the 1.3-kb repeat family.

### **Pot2: an inverted repeat transposon**

Pot2 (*Pyricularia oryzae* transposon) was isolated as an insertion within a member of the 1.3-kb repeat family. Restriction mapping and sequencing of a 3.2-kb derivative showed that the increase in size was due to the presence of an additional 1.8-kb DNA within the 1.3-kb repeat element (Fig. 3b). This extra piece of DNA (named Pot2) had 43-bp perfect inverted repeats at the end and 16-bp direct repeats within each inverted repeat (Kachroo et al 1994). Computer analysis showed the presence of a single open reading frame (ORF) coding for a putative protein of 535 amino acids. Analysis of the empty site, which corresponded to the insertion site of Pot2 within the 3.2-kb repeat, showed a duplication of dinucleotide TA at the target site. A target site analysis carried out by sequencing 12 random insertions revealed that TA dinucleotide was common to all. The insertion sequence Pot2 resembled the inverted repeat transposons from *Drosophila* (Mariner) and *Caenorhabditis elegans* (Tc1) in showing inverted repeats at the ends, duplication of dinucleotide TA at the target site, and the presence of a large ORF.

Data base comparison of the putative protein from Pot2 showed 40% identity to Fot1, an inverted repeat transposon from *Fusarium oxysporum*. The identity was maximum toward the middle of the protein. The two elements showed a high level of organizational similarity (Table 1). At the DNA level, a high degree of similarity was seen between the inverted repeats of Pot2 and Fot1, which were aligned into three domains of perfect identity. Both of these elements showed the presence of direct repeats within the inverted repeats, which appears to be a unique feature of this group of elements.

A very high level of conservation seen between Pot2 and Fot1 at the protein level and within TIRs indicate the presence of a new family of transposable elements that may be dispersed among fungi. The distribution of transposable elements among closely related or diverse species could be explained on the basis of vertical or horizontal transmission of genetic material. These mechanisms are not mutually exclusive and could account for the high level of sequence identity. This may represent parallel

**Table 1. Comparison between the inverted repeat transposons Pot2 and Fot1.**

	Pot2	Fot1
Size of the element	1.861 kb	1.928 kb
ORF, size of putative protein	535 aa	542 aa
Inverted repeats	43 bp	44 bp (imperfect by 1 bp)
Direct repeats	16 bp	13 bp
Copy number	~100	~100
Amino acid homology	39.3% identity to Pot1	39.3% identity to Pot2
Target site	Duplicate TA at target site	Duplicate TA at target site

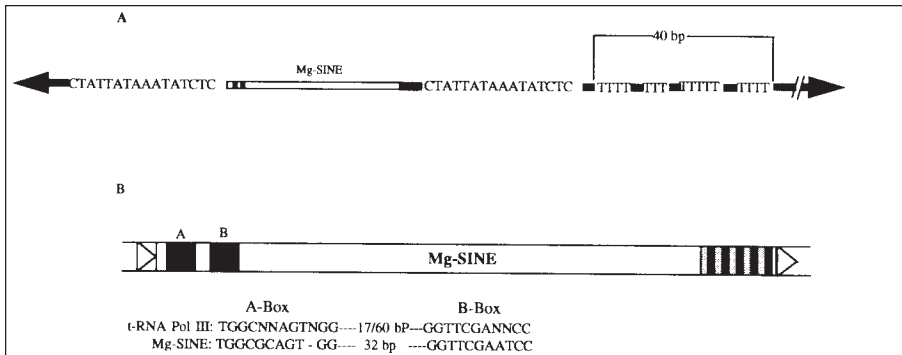
evolution of the two species, and in this context, it will be interesting to see if this group of elements is present in other closely related genera.

Isolation and characterization of another inverted repeat transposon, Impala, from *F. oxysporum* has revealed that, like retroelements, the inverted repeat transposons may also form multiple families in the filamentous fungi. Interestingly, Impala does not show any significant similarity with Fot1 either at the nucleotide level, particularly in the termini of the TIRs or at the amino acid level. This element also differs from Fot1 in a number of structural features although it appears to follow a similar mechanism of transposition leading to duplication of TA at the target site. In yet another study, another inverted repeat transposon has been recently characterized from *M. grisea*, which unlike Fot1 and Impala, shows a number of structural features similar to Pot2 (Farman et al 1996a).

### **Mg-SINE: short interspersed nuclear element**

Mg-SINE (*M. grisea* short interspersed nuclear element) was identified as an insertion within the inverted repeat transposon Pot2 (Kachroo et al 1995; Fig. 4a). Sequence analysis revealed the presence of both A and B box sequences with a perfect match with the tRNA polymerase III consensus. Mg-SINE showed the characteristic features of a generic SINE element that includes the presence of an RNA polymerase III consensus binding site, duplication of the target site, and an A-rich 3' end (Fig. 4b). The target site duplication of Mg-SINE elements was found to vary from 1 to 16 bp, as is also seen in the mammalian SINE elements. The A-rich region of Mg-SINE was represented by from five to nine copies of trinucleotide repeat TAC. Data base comparison showed a significant homology to tRNA of *Drosophila* and yeast, which was predominantly due to the conserved A and B box sequences.

Southern hybridization analysis of 35 isolates (Fig. 5; data shown for 12) obtained from different geographical regions showed that Mg-SINE is present in both rice and nonrice pathogens of *M. grisea*. Mg-SINE represents the third highly repetitive element characterized in the present study (including Pot2 and 1.3-kb repeats), which is ubiquitous in its distribution among different host-specific forms of *M. grisea*. This



**Fig. 4.** Schematic representation of Mg-SINE insertion in Pot2 (A) and the structure of the element (B). The sequence in A represents the 16-bp target site, which undergoes duplication upon retroposition of Mg-SINE. The target site is A/T rich consisting of 13 A/T residues. The sequence flanking the target site contains four consecutive rows of three or more Ts in a span of 40 bp, which can serve as potential terminators of RNA polymerase III. The open triangles in B represent direct repeats formed as a result of target site duplication. Dark boxes represent A and B box RNA polymerase III consensus sequence. Shaded box with vertical bars represents trinucleotide repeat region of Mg-SINE, each bar representing a single repeat unit.

result further strengthens our hypothesis of a common origin among rice and nonrice isolates. CHEF and quantitative dot blot analysis revealed that Mg-SINE, like Pot2 and 1.3-kb repeat elements, is dispersed at approximately 100 copies per haploid genome in both rice and nonrice isolates.

Both in vivo and in vitro studies, carried out with Alu and other related SINE families from the mammalian genome, have shown that the SINE elements are transcribed into an RNA by RNA polymerase III (Fuhrman et al 1981, Slagel and Deininger 1989). As proposed earlier (Deininger 1989), the retroposition of SINE elements depends on synthesis of cDNA by reverse transcriptase and, since these elements do not possess any ORFs, the reverse transcriptase function should be available in trans. Mg-SINE appears to be a functional element as judged by the presence of a transcript of approximately 0.5-kb size observed in Northern blot hybridization analysis. The presence of a functional retroelement Maggy in the genome of rice-infecting isolates has already been shown (Farman et al 1996b; M.H. Lebrun, B. Valent, F. Chumley, V. Shull, J.E. Hamer, unpubl. data) and it is likely that Mg-SINE uses the reverse transcriptase function of this retroelement to generate a copy of cDNA. The retroelement Maggy is present in all the rice-infecting pathogens analyzed and has a variable copy number in nonrice-infecting pathogens of *M. grisea* (Farman et al 1996b). A low copy number of Maggy in most nonrice pathogens makes it very likely that these pathogens possess an additional source of reverse transcriptase function, which would have assisted in amplification and dispersion of Mg-SINE. The presence of a retroelement Grh in *Eleusine* pathogens of *M. grisea* and a partial sequence of a repetitive DNA from rice pathogens, which shows identity to

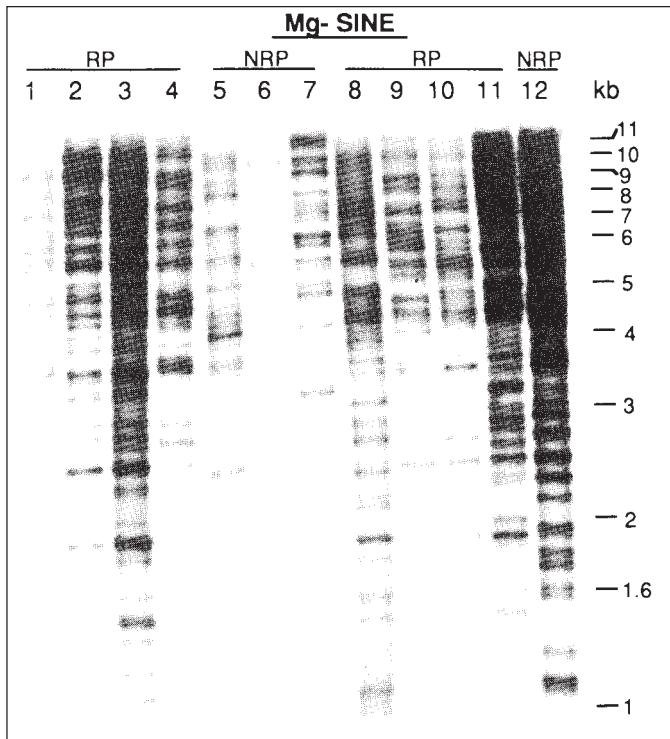


Fig. 5. Southern hybridization analysis of genomic DNA of rice and nonrice pathogens of *M. grisea* probes with Mg-SINE. Genomic DNA (2 g) was digested with *EcoRV*, electrophoresed through a 0.8% gel, transferred to MSI-nylon membrane, and hybridized with Mg-SINE. *EcoRV* does not have any site within Mg-SINE. The lanes contain DNA from: B101 (India), lane 1; B157 (India), lane 2; F (India), lane 3; 102 (Philippines), lane 4; Pr342 (Philippines), lane 5; Pr886 (Philippines), lane 6; Pg3393 (India), lane 7; 4360-17-1 (USA), lane 8; JMB840610 (Philippines), lane 9; 104 (Philippines), lane 10; B (India), lane 11; Ei 476 (Philippines), lane 12. RP and NRP designate rice pathogens and nonrice pathogens, respectively.

retroelements, is supportive of the above hypothesis (Dobinson et al 1993, Sone et al 1993).

The consensus transcription terminator of RNA polymerase III transcription is a sequence of four or more consecutive Ts, which have been shown to reside in the sequence flanking the SINE elements (Jagadeeswaran et al 1981, Deininger 1989). Analysis of the sequence flanking the Mg-SINE insertion in Pot2 revealed the presence of four blocks of Ts in a span of 40 bp downstream of the trinucleotide repeat at the 3' end (Fig. 4A). However, since different Mg-SINE elements would have a different

sequence flanking the 3' end, it is possible that these elements would result in transcripts of different lengths. This, in turn, would depend upon how far the poly T stretch is from the 3' end of Mg-SINE. Sequence analysis of various Mg-SINE elements revealed a high level of sequence conservation, suggesting that these may be generated by transcription of a master element as has been hypothesized for Alu members (Deininger et al 1992). Alternatively, various heterogeneous transcripts generated by Mg-SINE elements distributed throughout the genome may be processed to a uniform size followed by cDNA synthesis and integration within the genome. The self-priming reverse transcription process hypothesized for Alu elements (Jagadeeswaran et al 1981, Deininger 1989) cannot be used to explain the cDNA synthesis of Mg-SINE and other similar SINE elements whose 3' end sequence consists of di tri or tetra nucleotide repeats (Deininger 1989). However, it is also likely that the poly U sequence of the RNA Pol III transcript forms a partial loop upon base pairing with A and G residues (Wyatt et al 1989) of trinucleotide repeats of Mg-SINE. The position where the loop formation takes place could also result in generation of variable number of trinucleotide repeats as seen in Mg-SINE.

The secondary structure analysis of Mg-SINE showed a tRNA related, a tRNA unrelated, and an AT-rich region that is typical of mammalian SINE elements (Fig. 6). The 73 bp at the 5' end of Mg-SINE folds into a tRNA-like structure that terminates with nucleotides CCA, a characteristic feature of tRNA. The predicted secondary structure folds into D and TC loops corresponding to the A and B boxes of Mg-SINE, while the anticodon loop forms the middle arm, suggesting that Mg-SINE originated from a precursor tRNA. The absence of a short arm between the anticodon loop and the B box could be explained by sequence divergence. However, it appears likely that the precursor tRNA belongs to class I tRNAs, which have five nucleotides in the short arm as compared with class II which have a long extra loop region (Sakagami et al 1994).

Analysis of various cosmid clones, which hybridized to Mg-SINE, revealed that the ones hybridizing weakly to the probe contained a chimeric structure (Ch-SINE), which showed sequence homology to a 242-bp region at the 3' end of Mg-SINE while the 452-bp region at the 5' end was dissimilar to Mg-SINE. Alignment of the Ch-SINE and Mg-SINE sequence showed point mutations, insertions, and deletions of one or more bases in the SINE-like region of Ch-SINE, which have contributed to sequence divergence. The type II Galgo SINE family resembles Ch-SINE in being a chimeric element composed of sequences related to monomer family in its left half and sequences identical to Alu in the right half and has been proposed to have arisen as a result of fusion between a monomer family member and an Alu family member. The Ch-SINE does not contain the A and B box consensus sequence of RNA polymerase III promoter or direct repeats at the ends although it possesses the trinucleotide repeats at their 3' ends. Southern hybridization analysis carried out with DNA of both rice and nonrice pathogens of *M. grisea* shows that Ch-SINE is a moderately repetitive element present in both subgroups. Sequence analysis of two Ch-SINE elements showed that both contained a variable number of trinucleotide repeats at their 3' end. Whether this could be due to many such fusion events taking

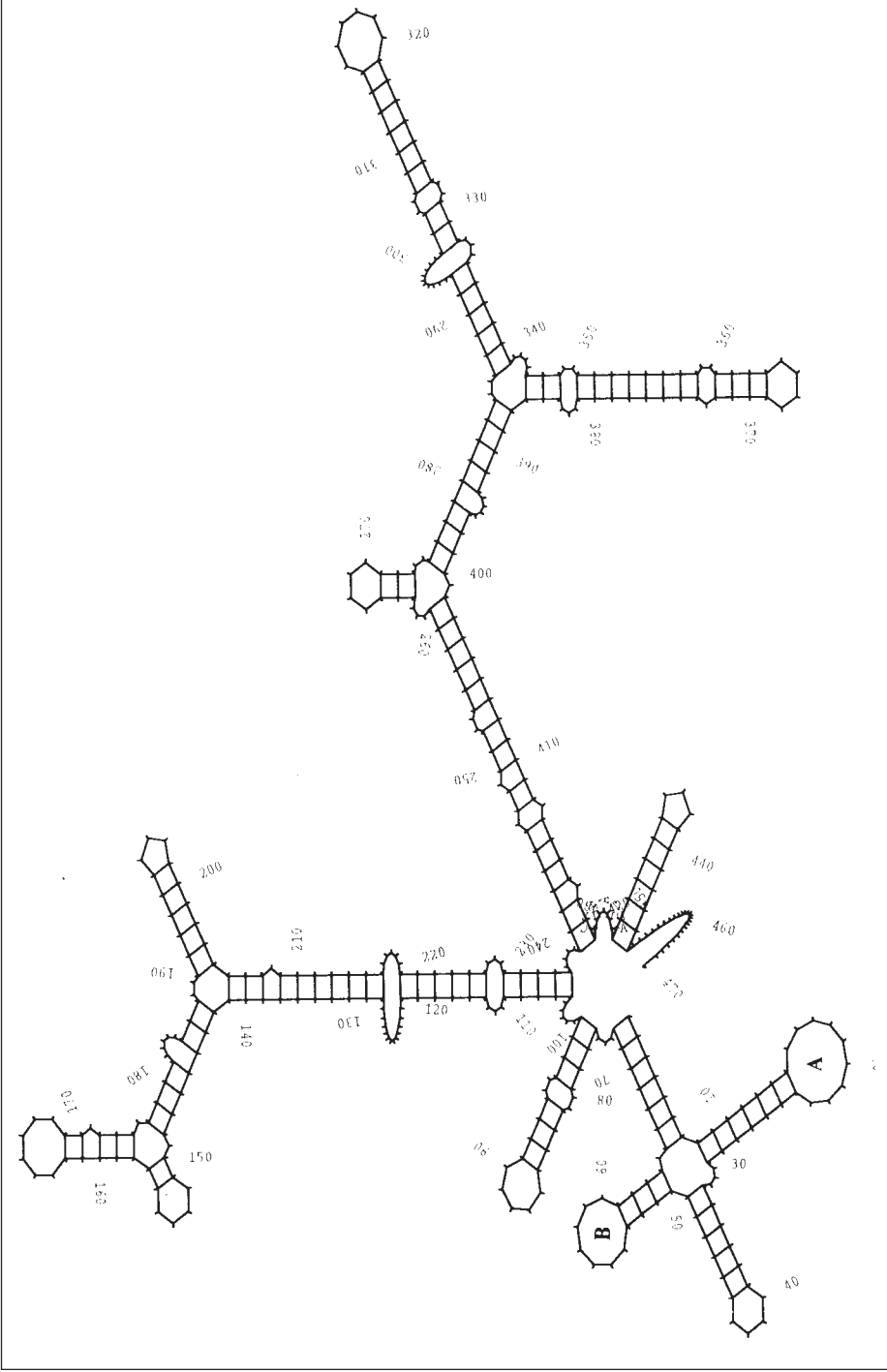


Fig. 6. Secondary structure analysis of Mg-SINE. The structural analysis was carried out using Squiggle and Fold programs of the University of Wisconsin Genetics Computer group programs (Devereux et al 1984). Numbers are given from the 5' end of Mg-SINE. A and B designate the conserved polymerase III consensus promoter sequence. The 1-73-bp region shows the cloverlike structure typical of tRNA while the rest of the structure is unrelated to tRNA.

place in the genome followed by their amplification or this element having a function similar to the SINE element, which generates a variable 3' end during their retroposition process, still remains an open question. Our recent studies have shown the presence of yet another LINE-like element in the genome of *M. grisea* which was isolated as an insertion into Mg-SINE and Ch-SINE elements indicating that such events may be of common occurrence in the genome of *M. grisea* (P. Kachroo, M. Ahuja, S. Leong, B. Chattoo, unpubl. data).

SINE elements occupy an important place among all the known groups of transposable elements. In addition to causing insertions and genomic rearrangements, these have been speculated to have a variety of other functions including organization of chromatin structure, RNA processing/stability, and a role in replication and transcription (Deininger 1989). Their ability to mobilize other sequences in the genome by undergoing fusion with them is also a unique feature known only for SINE elements (Weiner et al 1986). Most studies on SINE elements have been carried out in mammalian systems although their presence has been shown in tobacco (Yoshioka et al 1993), rice (Mochizuki et al 1992) and *Drosophila* (Weiner et al 1986). Our present study clearly demonstrates that these elements share a high level of structural similarity, irrespective of their phylogenetic position. The presence of repetitive DNA having SINE-like properties in obligate parasite *Erysiphe graminis* (Rasmussen et al 1993) further indicates that SINE elements may be of common occurrence in the genome of phytopathogenic fungi. A detailed study involving elucidation of their role in genome rearrangements will therefore be helpful in understanding the molecular basis of genome variability among phytopathogenic fungi.

## Cited references

- Coen ES, Thoday JM, Dover G. 1982. Rate of turnover of structural variants in the rDNA gene family of *Drosophila melanogaster*. *Nature* 295:564-568.
- Deininger PL. 1989. SINES: short interspersed DNA elements in higher eukaryotes. In: Berg DE, Howe MM, editors. *Mobile DNA*. Washington, D.C.(USA): American Society for Microbiology. p 619-636.
- Deininger PL, Batzer MA, Hutchinson CA III, Edgell MH. 1992. Master genes in mammalian repetitive DNA amplifications. *Trends Genet.* 8:307-311.
- Devereux J, Haerberli P, Smithies O. 1984. A comprehensive set of sequence analysis programs for the VAX. *Nucleic Acids Res.* 12:387-389.
- Dobinson KF, Harris RE, Hamer JE. 1993. Grasshopper, a long terminal repeat (LTR) retroelement in the phytopathogenic fungus *Magnaporthe grisea*. *Mol. Plant-Microbe Interact.* 6:114-126.
- Farman ML, Taura S, Leong SA. 1996a. The *Magnaporthe grisea* DNA fingerprinting probe, MGR586, contains the 3' end of an inverted transposon. *Mol. Gen. Genet.* (in press)
- Farman ML, Tosa Y, Nitta N, Leong SA. 1996b. Maggy, a retrotransposon in the genome of the rice blast fungus, *Magnaporthe grisea*. *Mol. Gen. Genet.* (in press)
- Fedoroff NV. 1979. On spacers. *Cell* 16:697-710.
- Fuhrman S, Deininger PL, LaPorte P, Friedmann T, Geiduschek EP. 1981. Analysis of transcription of the human Alu family ubiquitous repeating elements by eukaryotic RNA polymerase III. *Nucleic Acids Res.* 9:6439-6457.

- Giatgong P, Frederiksen RA. 1969. Pathogenic variability and cytology of monoconidial subcultures of *Pyricularia oryzae*. *Phytopathology* 59:1152-1157.
- Hamer JE, Farrall L, Orbach MJ, Valent B, Chumley FG. 1989. Host species-specific conservation of a family of repeated DNA sequences in the genome of a fungal plant pathogen. *Proc. Natl. Acad. Sci. USA* 86:9981-9985.
- Jagadeeswaran P, Forget BG, Weissman SM. 1981. Short interspersed repetitive DNA elements in eukaryotes: transposable DNA elements generated by reverse transcription of RNA Pol III transcripts? *Cell* 26:141-142.
- Kachroo P, Leong SA, Chattoo BB. 1994. Pot2, an inverted repeat transposon from the rice blast fungus *Magnaporthe grisea*. *Mol. Gen. Genet* 235:339-338.
- Kachroo P, Leong SA, Chattoo BB. 1995. Mg-SINE: A short interspersed nuclear element from the rice blast fungus *Magnaporthe grisea*. *Proc. Natl. Acad. Sci. USA* 92:11125-11129.
- Latterell FM. 1975. Phenotypic stability of pathogenic races of *Pyricularia oryzae*, and its implications for breeding of blast resistant varieties. In: *Proceedings of a Seminar on Horizontal Resistance to the Blast Disease of Rice*. Cali, Colombia: Centro Internacional de Agricultura Tropical. p 199-234.
- Leong SA, Farman ML, Budde AD, Smith RJ, Tosa Y, Nitta N, 1994. Molecular genetic approach to the study of cultivar specificity in the rice blast fungus. In: Zeigler RS, Leong SA, Teng PS, editors. *Rice blast disease*. Wallingford (UK): CAB International. p 87-110.
- Mochizuki K, Umeda M, Ohtsubo H, Ohtsubo E. 1992. Characterization of a plant SINE, p-SINE1, in rice genomes. *Jpn. J. Genet.* 57:155-166.
- Ou SH. 1985. In: *Rice diseases*. Kew (UK): Commonwealth Mycological Institute. p 109-201.
- Petes TD. 1980. Unequal meiotic recombination with tandem arrays of yeast ribosomal DNA genes. *Cell* 19:765-774.
- Rasmussen M, Rossen L, Giese H. 1993. SINE-like properties of a highly repetitive element in the genome of the obligate parasitic fungus *Erysiphe graminis* f.sp. *hordei*. *Mol. Gen. Genet.* 239:298-303.
- Rothstein R, Helms C, Rosenberg N. 1987. Concerted deletions and inversions are caused by mitotic recombination between delta sequences in *Saccharomyces cerevisiae*. *Mol. Cell Biol.* 7:1198-1207.
- Sakagami M, Oshima K, Mukoyama H, Yasne H, Okada N. 1994. A novel tRNA species as an origin of short interspersed repetitive elements (SINEs). *J. Mol. Biol.* 239:731-735.
- Skinner DZ, Budde AD, Farman ML, Smith JR, Leung H, Leong SA. 1993. Genome organization of *Magnaporthe grisea*: genetic map, electrophoretic karyotype and occurrence of repeated DNAs. *Theor. Appl. Genet* 87:545-557.
- Slagel VK, Deininger PL. 1989. In vivo transcription of a cloned prosimian SINE sequence. *Nucleic Acids Res.* 17:8669-8682.
- Sone T, Suto M, Tomita F. 1993. Host species-specific repetitive DNA sequence in the genome of *Magnaporthe grisea*, the rice blast fungus. *Biosci. Biotechnol. Biochem.* 57:1228-1230.
- Weiner AM, Deininger PL, Efstratiadis A. 1986. Nonviral retroposons: genes, pseudogenes, and transposable elements generated by the reverse flow of genetic information. *Annu. Rev. Biochem.* 55:631-661.
- Wyatt RJ, Puglisi JD, Tinoco Jr I. 1989. RNA folding: Pseudoknots, loops and bulges. *BioEssays* 11:100-106.
- Yamasaki Y, Niizeki H. 1965. Studies on variation of the rice blast fungus *Pyricularia oryzae* Cav. I. Karyological and genetical studies on variation. *Bull. Natl. Inst. Agric. Sci.* 13:231-274.

Yoshioka Y, Matsumoto S, Kojima S, Ohshima K, Okada N, Machida Y. 1993. Molecular characterization of a short interspersed repetitive element from tobacco that exhibits sequence homology to specific tRNAs. Proc. Natl. Acad. Sci. USA 90:6562-6566.

## Notes

*Authors' addresses:* P. Kachroo, Department of Microbiology and Biotechnology Centre, Faculty of Science, M.S. University, Baroda 390 002, India (current address: Department of Plant Pathology, 1630 Linden Drive, Madison, WI 53706, USA); S.A. Leong, Department of Plant Pathology and USDA-ARS Plant Disease Resistance Research Unit, 1630 Linden Drive, Madison, WI 53706, USA; B.B. Chattoo, Department of Microbiology and Biotechnology Centre, Faculty of Science, M.S. University, Baroda 390 002, India.

*Acknowledgments:* This work was supported by grants from the Rockefeller Foundation and the U. S. Department of Agriculture to and by the Rockefeller Foundation and Department of Biotechnology, Government of India, to BBC.

*Citation:* [IRRI] International Rice Research Institute. 1996. Rice genetics III. Proceedings of the Third International Rice Genetics Symposium, 16-20 Oct 1995. Manila (Philippines): IRRI.