Detection of a Simplex RAPD Marker Linked to Resistance to Potato Virus Y in a Tetraploid Potato

Kazuyoshi Hosaka[1]*, Yuko Hosaka[1], Motoyuki Mori[2], Tsutomu Maida[3], and Hiroshi Matsunaga[4]

[1]Experimental Farm, Kobe University, 1348 Uzurano, Kasai, Hyogo 675-2103, Japan.
[2]Hokkaido National Agricultural Experiment Station, Shinsei, Memuro, Kasai, Hokkaido 082-0071, Japan.
[3]National Center for Seeds and Seedlings, Unzen Station, 1494-34 Saigo Bo, Mizuho, Minamitakaki, Nagasaki 859-1211, Japan.
[4]Hokkaido Prefectural Tokachi Agricultural Experiment Station, Shinsei, Memuro, Kasai, Hokkaido 082-0071, Japan.
Corresponding author: Tel: 81-790-49-3121; Fax: 81-790-49-0343; E-mail: hosaka@kobe-u.ac.jp.

ABSTRACT

Extreme resistance to potato virus Y, derived from a wild diploid species *Solanum chacoense*, was found in Japanese cultivar Konafubuki. The segregation ratio of resistant vs susceptible in the tetraploid population from Kita-akari (susceptible) x Konafubuki (resistant) indicated that the resistance gene followed a monogenic dominant fashion. Bulked DNA samples of resistant and of susceptible clones were screened with 306 decamer primers by PCR to find RAPD markers linked to the resistance. The RAPD marker 38-530 was reproducibly detected in the resistant clones with a recombination frequency of 16.3%. Except for Konafubuki the marker band was found only in a few limited parental lines and cultivars where the resistance is not involved. Thus, using Konafubuki as a resistance gene source, the RAPD marker 38-530 would be practically and widely useful in tetraploid breeding programs.

RESUMEN

En el cultivar japonés "Konafubuki" se encontró resistencia extrema al virus de la papa Y, derivada de una especie silvestre diploide de *Solanum chacoense*. El rango de segregación de la resistencia vs. la susceptibilidad en la población tetraploide de "Kita-akari" (susceptible) x "Konafubuki" (resistente) indicó que el gen de resistencia siguió un patrón dominante monogénico. Muestras agrupadas de mezclas de ADN de resistencia y de clones susceptibles fueron tamizadas usando 306 iniciadores decaméricos por PCR (Reacción on cadena de la polimerasa) para encontrar marcadores de RAPD vlnculados a la resistencia Se descubrió cierto grado de reproducción en clones resistentes del marcador RAPD 38-530 con una frecuencia de recombinación del 16.3%. A excepción de "Konafubuki", la banda del marcador se encontró sólo en unas pocas lineas parentales y cultivares donde no estaba implicada la resistencia.. Así, usando "Konafubuki" como fuente genética de restencia, el marcador RAPD 38-530 sería muy útil en los programas de mejoramiento de tetraploides.

INTRODUCTION

Molecular marker-assisted selection may facilitate quick advances in potato breeding. Molecular marker-based genetic maps of potato have been constructed (Bonierbale *et al.* 1988; Gebhardt *et al.* 1989, 1991; Tanksley *et al.* 1992; Jacobs *et al.* 1995; van Eck *et al.* 1995). Several important disease and nematode resistance genes have been mapped on these maps: resistance genes to *Phytophthora infestans* (Leonards-Schippers *et al.* 1992; El-Kharbotly *et al.* 1994, 1996), potato virus X (Ritter *et al.* 1991), potato virus Y (Brigneti *et al.* 1997; Hämäläinen *et al.* 1997), cyst nematode (Barone *et al.* 1990; Gebhardt *et al.* 1993; Pineda *et al.* 1993; Kreike *et al.* 1994; Rouppe van der Voort *et al.* 1997, 1998), and root-knot nematode (Rouppe van der Voort *et al.* 1999). The linked markers for these resistance genes are either restriction fragment length polymorphism (RFLP) or amplified fragment length polymorphism (AFLP) markers found exclusively using diploid segregating populations.

If a diploid induced from a tetraploid potato has an RFLP genotype of Aa, the RFLP genotype of its original tetraploid parent must be either one of Aaaa, AAaa, or AAAa. In the case that the resistance gene is linked in coupling phase with A at diploidy, we can assume that the resistance gene is also linked with A at tetraploidy and we can use the marker for indirect selection in tetraploid breeding. However, if the resistance gene at tetraploidy is located only in one A chromosome of AAaa (or one or two A chromosomes in AAAa), there would be one chromosome marked by the A RFLP marker actually linked with the resistance gene and another choromosome(s) also marked by

Accepted for publication December 11, 2000.
ADDITIONAL KEY WORDS: PVY, single dominant gene, bulked segregant analysis, breeding.

the same RFLP marker but not linked with the resistance gene. Then, this marker would not be highly effective as a selection marker for selection in the source tetraploid population. Thus, not all linked markers found using diploid mapping populations are usable as selection markers for tetraploids (Niewöhner *et al.* 1995). Tetraploid segregating populations are sometimes available from breeding programs, although the genetics is much complicated due to autotetraploidy. Only the mating type of simplex x nulliplex (Aaaa x aaaa) can bring about simple phenotypic segregation 1A:1a by a random chromosome assortment model, or 0.87A:1a by a random chromatid assortment model. From the segregating population of this mating type, a linked marker in coupling phase can be obtained.

Random amplified polymorphic DNA (RAPD) markers are PCR-based DNA markers detected by one of the simplest procedures using a small amount of leaf tissues (Williams *et al.* 1991). Combining RAPD technology with bulked DNA samples, linked markers can be rapidly identified (bulked segregant analysis, Michelmore *et al.* 1991). However, RAPD markers have rarely been used for mapping genes in potato. RAPD phenotypes are often influenced by various factors, causing reproducibility problems (Skroch and Nienhuis 1995; Staub *et al.* 1996).

A Japanese cultivar, Konafubuki, showed extreme resistance to one of the major viruses, potato virus Y (PVY) of potato. The resistance was originally descended from a wild diploid species *Solanum chacoense* (Asama *et al.* 1982; Anonymous 1986). In this paper, a highly reproducible RAPD marker linked to the PVY resistance gene is found using a tetraploid population produced from a mating type of simplex x nulliplex, and its utility in Japanese breeding program is discussed.

TABLE 1—*Phenotypic frequencies of the RAPD marker 38-530 and the goodness-of-fit to expected segregation ratios for random chromosome assortment and random chromatid assortment models.*

		38-530		$x2$ value	
Hybrid progeny	No.	+	-	1:1	0.87:1
Kita-akari x Konafubuki	100	41	59	3.24	1.23
Kon-iku 23 x WB66201-10	25	10	15	1.00	0.43
Kon-iku 24 x WB66201-10	13	6	7	0.08	<0.01
Kon-kei 57 x WB66201-10	21	10	11	0.05	<0.01
Total	159	67	92	3.93*	1.23

*indicates significant ($P<0.05$) deviation from expected segregation.

TABLE 2—*Potato cultivars that exhibited the RAPD marker 38-530 (star-marked).*

(1) Cultivars bred in Japan
Beni-akari, Benimaru, Bifukabeni, Bifukashiro, Bihoro*, Chijiwa, Chitose, Dejima, Eniwa, Ezo-akari, Hatsufubuki*, Hokkai-aka, Hokkaikogane, Hokkaishiro, Jaga Kids Red '90, Jaga Kids Purple '90, Kita-akari, Konafubuki*, Meihou, Musamaru, Myojo, Neodelicious, Niseko, Nishiyutaka, Norin 1, Norin 2, Oojiro, Red Echo, Rishiri*, Sakurafubuki*, Setoyutaka, Shimabara, Shiretoko, Tachibana, Tarumae, Touya, Toyo-akari*, Toyoshiro, Unzen, Waseshiro, Yellow Shark, Yoraku*, Yukijiro

(2) Cultivars bred outside Japan
Atlantic, Bintje, Early Rose, Gemchip, Gineke, Irish Cobbler, Kanona, Katahdin, May Queen, ND860-2, Norking Russet, Pepo, Russet Burbank, Snowden, Tunika, Yankee Chipper

MATERIALS AND METHODS

Plant Materials

The F_1 hybrid progeny of Kita-akari x Konafubuki and 3 F_1 hybrid progenies of different breeding lines x WB66201-10 were used for segregation analyses (Table 1). WB66201-10 as a male parent donated the PVY resistance to Konafubuki (Asama *et al.* 1982; Anonymous 1986). All Japanese cultivars, some major foreign cultivars, and some parental lines (Table 2, Figure 3) were used to investigate usefulness of the marker found.

Evaluation of PVY Resistance

The PVY-T (synonym of PVY^n) strain was inoculated mechanically to Kita-akari, Konafubuki and their F_1 plants 1 month after planting and the second inoculation was performed 2 wk later (primary infection). Two weeks after the second inoculation, leaves were sampled and frozen for ELISA test. Harvested tubers were re-planted in the following season, and the symptoms were recorded (secondary infection). Forty days after planting, ELISA test was performed. The double-antibody sandwich method was used for ELISA test (DAS-ELISA). Immunoplate wells were incubated with 1.25 µg/ml IgG (γ-globulin) for 4 hr at 37 C. Incubation with enzyme-conjugate was done at a concentration of 1.25 µg/ml for 3 hr at 37 C.

DNA Isolation, PCR, and Electrophoresis

Genomic DNA was isolated by the method of Doyle and

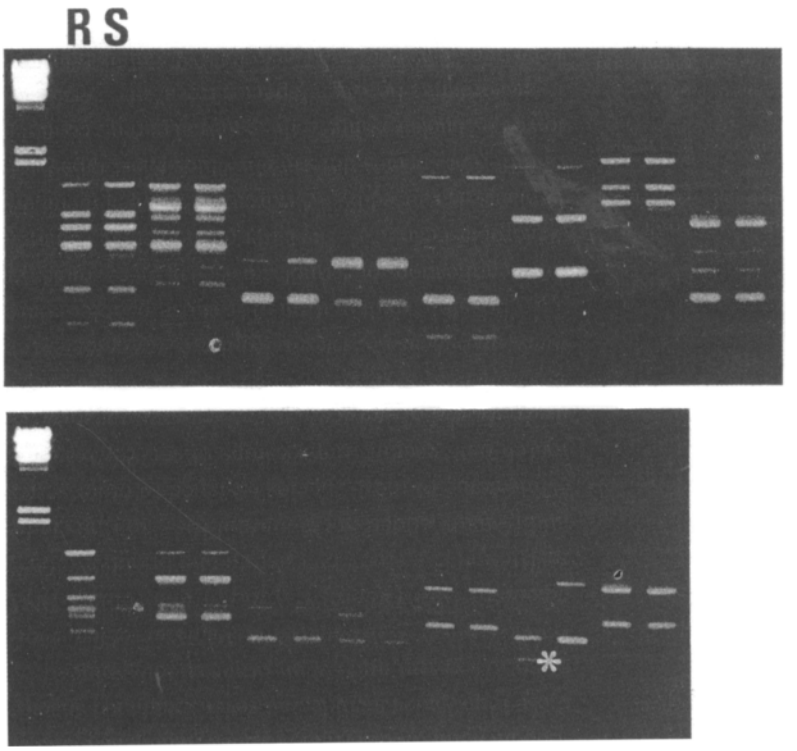

FIGURE 1.
Bulked segregant analysis with different decamer primers against a resistant DNA bulk (R) and a susceptible DNA bulk (S). The marker band 38-530 is shown by a star-mark. Decamer primers screened were; (from top left) primer No. 314 (5'-CAGCGACTGT-3'), No. 315 (5'-AAGCGACCTG-3'), No. 316 (5'-CATTGGGGAG-3'), No. 317 (5'-GGTGAGGTCA-3'), No. 318 (5'-GTCCGTACTG-3'), No. 319 (5'-GGTGCTCCGT-3'), No. 320 (5'-GGCACGTAAG-3'), No. 321 (5'-ACGTAGCGTC-3'), No. 30 (5'-CGGTCACTGA-3'), No. 31 (5'-GGGTCACTGA-3'), No. 33 (5'-TGGTGAGTGA-3'), No. 36 (5'-TGGTGACCGA-3'), No. 37 (5'-TGGTGACAGA-3'), No. 38 (5'-TTCGAGCCAG-3'), and No. 39 (5'-GTGAGGCGTC-3').

Doyle (1987). PCR amplification and electrophoresis was performed as described previously (Hosaka and Hanneman 1994).

RESULTS AND DISCUSSION

Resistance to PVY in a Hybrid Progeny

Konafubuki was extremely resistant to PVY-T, while Kitaakari was susceptible, showing significantly high absorbent values by ELISA test and leaf lesions by primary infection and crinkled leaves by secondary infection. Of 100 F_1 plants of Kitaakari x Konafubuki, 48 showed no symptom and significantly lower ELISA values in both primary and secondary infection, and thus were judged resistant. Forty-four showed various symptoms (mosaic, crinkled, stipple-streak, early died, rugose, and leaf lesion) and significantly higher ELISA values in either primary or secondary infection. These were judged susceptible. The remaining eight plants were not determined because they showed only ambiguous ELISA values or symptoms in primary infection. The segregation ratio of 48 resistant vs 44 susceptible plants did not significantly deviate from the expected segregation for Aaaa x aaaa; 1:1 by a random chromosome assortment model (x^2 = 1.42, 0.3>P>0.2) and 0.87:1 by a random chromatid assortment model (x^2 = 3.38, 0.1>P>0.05). Thus, it appears that the dominant gene (named Ry_{chc}) conferred resistance to PVY and is maintained in a simplex fashion in Konafubuki.

Bulked Segregant Analysis

Equal amounts of DNA samples each from 46 resistant plants and from 35 susceptible plants were mixed to make a sample set of PVY-R and PVY-S, respectively. This sample set was screened against a total of 306 decamer primers (Figure 1). Three primers showed specific bands to PVY-R not visibly detected in PVY-S. These primers were preliminarily examined for linkage with eight resistant and eight susceptible plants. Two of them did not show apparent correlation between the band and resistance. The primer No. 38 (5'-TTCGAGCCAG-3', = OPC-01 of Operon Technologies Inc., Alameda CA, USA) generated a clear band potentially linked to resistance (Figure 2). This band is designated as 38-530 for the band size was estimated to be approximately 530 base pairs. This marker has previously been used for Japanese cultivar identification under the name 38d in Mori *et al.* (1993).

Segregation of 38-530 in Tetraploid Progenies

The segregation of 38-530 was analyzed in four tetraploid progenies (Table 1). In all the progenies, ratios of presence vs absence fit the expected ratio for the progeny of simplex x nul-

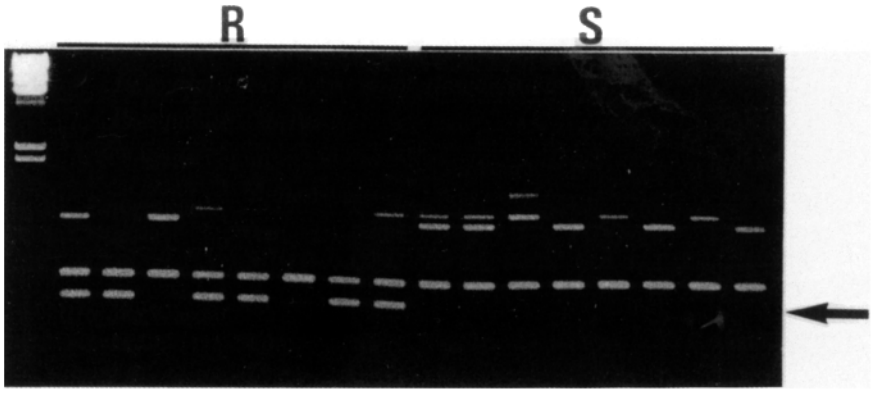

FIGURE 2.
Association of resistant (R) and susceptible (S) genotypes in F_1 progeny of Kita-akari x Konafubuki with the RAPD marker 38-530 (arrowed).

liplex. The ratio of the cumulative numbers of four progenies significantly deviated at a 5% level from the expected ratio by a random chromosome assortment model, but fit to the ratio by a random chromatid assortment model.

Linkage between 38-530 and PVY resistance

Of 92 F_1 plants of Kita-akari x Konafubuki, 36 resistant plants had the 38-530 marker, while 41 susceptible plants did not. On the other hand, 12 resistant plants did not have the marker, while three susceptible plants did. Thus, 15 plants were detected as recombinants (a recombination frequency of 16.3%).

Pedigree of 38-530 and PVY Resistance

The pedigree information of Konafubuki is shown in Figure 3a. Parental lines were traced back in terms of the 38-530 marker. Although W584454-1 was not available, it is estimated to be a donor of the 38-530 marker to WB60015-7. Likewise, the donor of the 38-530 marker to W584454-1 can be assumed to be

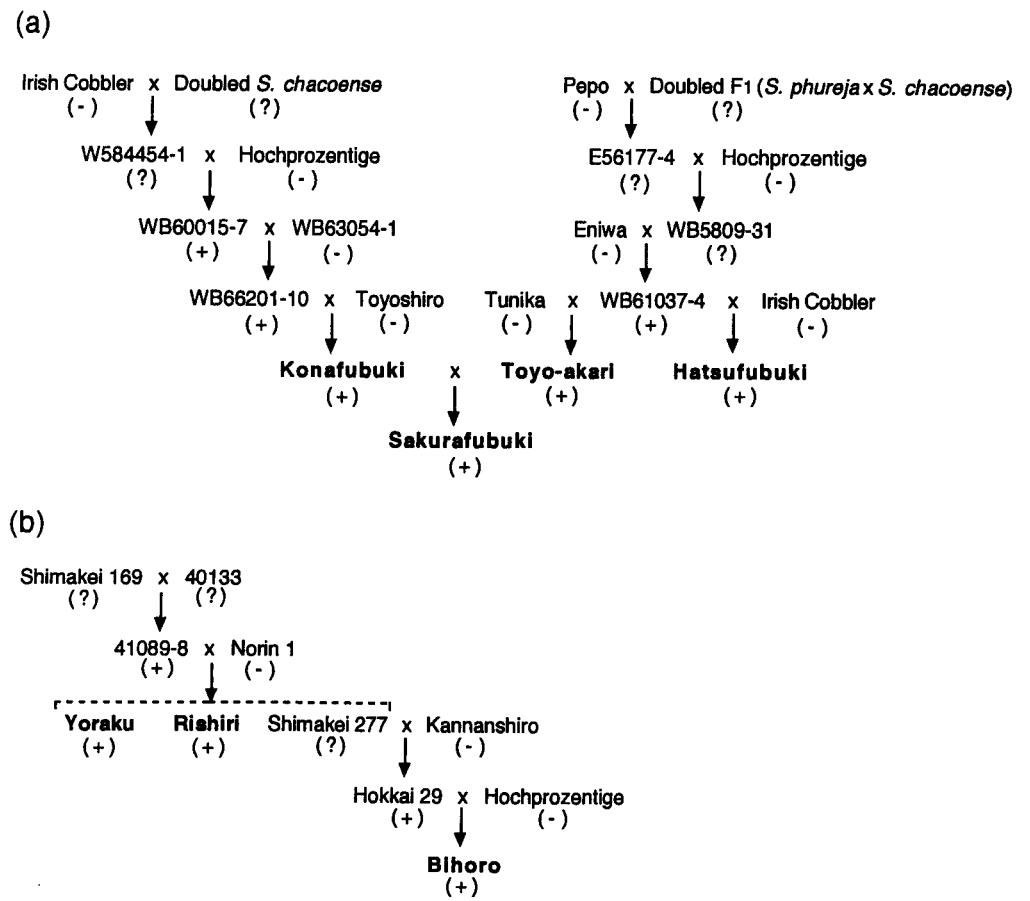

FIGURE 3.
Pedigree of Japanese cultivars that have the RAPD marker 38-530. Presence (+), absence (-), or unknown (?) of the marker for each clone is presented in parenthesis.

"doubled *S. chacoense*," which donated PVY resistance to Konafubuki. Therefore, it is likely that the 38-530 marker was derived together with and linked with the Ry_{chc} gene from *S. chacoense* to Konafubuki.

Distribution of 38-530 among Cultivars

Among 43 Japanese and 16 foreign cultivars, the RAPD marker 38-530 was found in Konafubuki and six other cultivars (Bihoro, Hatsufubuki, Rishiri, Sakurafubuki, Toyo-akari, and Yoraku) (Table 2). These cultivars are related to each other as shown in Figure 3. The marker band of Hatsufubuki, Konafubuki, Sakurafubuki, and Toyo-akari were possibly derived from *S. chacoense* (Figure 3a). The marker band of Bihoro, Rishiri, and Yoraku was obviously derived from 41089-8 (Figure 3b), but the parent donating the marker band to 41089-8 was unknown because both parents were not available to this study.

Usefulness of the 38-530 Marker

Although RAPD assay is a PCR-based technique being relatively simple and cost-effective, the reproducibility has been problematic (Skroch and Nienhuis 1995; Staub *et al.* 1996). The RAPD marker 38-530 was easily detectable as seen in Figures 1 and 2, and highly reproducible over different conditions (data not shown).

The genetic recombination frequency (16.3%) between the Ry_{chc} gene and the RAPD marker 38-530 does not indicate very tight linkage. However, erroneous determination caused by recombination may be compensated by quick determination of possible resistant phenotypes by RAPD assay in practical breeding, because in this study the evaluation test for PVY took two seasons, nevertheless, eight out of 100 plants were still undetermined due to ambiguous ELISA values.

Two other extreme resistance genes to PVY have been known, Ry_{sto} (derived from *S. stoloniferum*) and Ry_{adg} (from *S. tuberosum* ssp. *andigena*), and both have been mapped on chromosome 11 (Brigneti *et al.* 1997; Hämäläinen *et al.* 1997). For the Ry_{adg} gene, a sequence-characterized amplified region (SCAR) marker has been developed, which enables simple detection of the marker by PCR (Kasai *et al.* 2000). The present extreme resistance gene (Ry_{chc}) was derived from *S. chacoense* (Asama *et al.* 1982; Anonymous 1986). Considering that the RAPD marker 38-530 has been mapped on chromosome 9 in the F_2 population of *S. chacoense* x *S. phureja* (Hosaka unpublished), the Ry_{chc} gene is probably different from the Ry_{sto} or Ry_{adg}. Thus, the RAPD marker 38-530 can monitor the new extreme resistance gene in tetraploid breeding.

In conclusion, the RAPD marker 38-530 would be useful in practical tetraploid breeding programs because the marker (1) was reproducibly detected by a simple technique, (2) could monitor the Ry_{chc} gene in tetraploid populations, and (3) would be widely used with Konafubuki as a resistance gene source because except for Konafubuki the marker band was found only in a few limited parental lines and cultivars where the resistance is not involved.

ACKNOWLEDGMENTS

We thank Prof. K. Kawano, Kobe University, for reading of the manuscript and useful comments, and Mr. S. Yoshida, Mr. T. Yamashita and Mr. K. Maruyama for maintenance of plant materials. This work was supported in part by Nagasaki Pref. Agricultural & Forestry Experiment Station, Nagasaki, Japan, and Calbee Potato, Inc., Tokyo, Japan.

LITERATURE CITED

Anonymous. 1986. Report of Plant Genetic Resources in Hokkaido, Japan. Part 3 Potato. Hokkaido Natl Agr Exp Stn, Miscellaneous Publication 29:57-76.

Asama, K., H. Ito, N. Murakami, and T. Itoh. 1982. New potato variety "Konafubuki". Bull Hokkaido Pref Agr Exp Stn 48:75-84.

Barone, A., E. Ritter, U. Schachtschabel, T. Debener, F. Salamini, and C. Gebhardt. 1990. Localization by restriction fragment length polymorphism mapping in potato of a major dominant gene conferring resistance to the potato cyst nematode *Globodera rostochiensis*. Mol Gen Genet 224:177-182.

Bonierbale, M.W., R.L. Plaisted, and S.D. Tanksley. 1988. RFLP maps based on a common set of clones reveal modes of chromosomal evolution in potato and tomato. Genetics 120:1095-1103.

Brigneti, G., J. Garcia-Mas, and D.C. Baulcombe. 1997. Molecular mapping of the potato virus Y resistance gene Ry_{sto} in potato. Theor Appl Genet 94:198-203.

Doyle, J.J., and J.L. Doyle. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochem Bull 19:11-15.

El-Kharbotly, A., C. Leonards-Schippers, D.J. Huigen, E. Jacobsen, A. Pereira, W.J. Stiekema, F. Salamini, and C. Gebhardt. 1994. Segregation analysis and RFLP mapping of the *R1* and *R3* alleles conferring race-specific resistance to *Phytophthora infestans* in progeny of dihaploid potato parents. Mol Gen Genet 242:749-754.

El-Kharbotly, A., C. Palomino-Sánchez, F. Salamini, E. Jacobsen, and C. Gebhardt. 1996. *R6* and *R7* alleles of potato conferring race-specific resistance to *Phytophthora infestans* (Mont.) de Bary identified genetic loci clustering with the *R3* locus on chromosome XI. Theor Appl Genet 92:880-884.

Gebhardt, C., D. Mugniery, E. Ritter, F. Salamini, and E. Bonnel. 1993. Identification of RFLP markers closely linked to the *H1* gene conferring resistance to *Globodera rostochiensis* in potato. Theor Appl Genet 85:541-544.

Gebhardt, C., E. Ritter, T. Debener, U. Schachtschabel, B. Walkemeier, H. Uhrig, and F. Salamini. 1989. RFLP analysis and linkage mapping in *Solanum tuberosum*. Theor Appl Genet 78:65-75.

Gebhardt, C., E. Ritter, A. Barone, T. Debener, B. Walkemeier, U. Schachtschabel, H. Kaufmann, R.D. Thompson, M.W. Bonierbale, M.W. Ganal, S.D. Tanksley, and F. Salamini. 1991. RFLP maps of potato and their alignment with the homoeologous tomato genome. Theor Appl Genet 83:49-57.

Hämäläinen, J.H., K.N. Watanabe, J.P.T. Valkonen, A. Arihara, R.L. Plaisted, E. Pehu, L. Miller, and S.A. Slack. 1997. Mapping and marker-assisted selection for a gene for extreme resistance to potato virus Y. Theor Appl Genet 94:192-197.

Hosaka, K., and R.E. Hanneman Jr. 1994. Random amplified polymorphic DNA markers detected in a segregating hybrid population of *Solanum chacoense* x *S. phureja*. Jpn J Genet 69:53-66.

Jacobs, J.M.E., H.J. Van Eck, P. Arens, B. Verkerk-Bakker, B. te Lintel Hekkert, H.J.M. Bastiaanssen, A. El-Kharbotly, A. Pereira, E. Jacobsen, and W.J. Stiekema. 1995. A genetic map of potato (*Solanum tuberosum*) integrating molecular markers, including transposons, and classical markers. Theor Appl Genet 91:289-300.

Kasai, K., Y. Morikawa, V.A. Sorri, J.P.T. Valkonen, C. Gebhardt, and K.N. Watanabe. 2000. Development of SCAR markers to the PVY resistance gene Ry_{adg} based on a common feature of plant disease resistance genes. Genome 43:1-8.

Kreike, C.M., J.R.A. De Koning, J.H. Vinke. J.W. Van Ooijen, and W.J. Stiekema. 1994. Quantitatively inherited resistance to *Globodera pallida* is dominated by one major locus in *Solanum spegazzinii*. Theor Appl Genet 88:764-769.

Leonards-Schippers, C., W. Gieffers, F. Salamini, and C. Gebhardt. 1992. The *R1* gene conferring race-specific resistance to *Phytophthora infestans* in potato is located on potato chromosome V. Mol Gen Genet 233:278-283.

Michelmore, R.W., I. Paran, and R.V. Kesseli. 1991. Identification of markers linked to disease-resistance genes by bulked segregant analysis: A rapid method to detect markers in specific genomic regions by using segregating populations. Proc Natl Acad Sci USA 88:9828-9832.

Mori, M., K. Hosaka, Y. Umemura, and C. Kaneda. 1993. Rapid identification of Japanese potato cultivars by RAPDs. Jpn J Genet 68:167-174.

Niewöhner, J., F. Salamini, and C. Gebhardt. 1995. Development of PCR assays diagnostic for RFLP marker alleles closely linked to alleles *Gro1* and *H1*, conferring resistance to the root cyst nematode *Globodera rostochiensis* in potato. Mol Breed 1:65-78.

Pineda, O., M.W. Bonierbale, R.L. Plaisted, B.B. Brodie, and S.D. Tanksley. 1993. Identification of RFLP markers linked to the *H1* gene conferring resistance to the potato cyst nematode *Globodera rostochiensis*. Genome 36:152-156.

Ritter, E., T. Debener, A. Barone, F. Salamini, and C. Gebhardt. 1991. RFLP mapping on potato chromosomes of two genes controlling extreme resistance to potato virus X (PVX). Mol Gen Genet 227:81-85.

Rouppe van der Voort, J., P. Wolters, R. Folkertsma, R. Hutten, P. van Zandvoort, H. Vinke, K. Kanyuka, A. Bendahmane, E. Jacobsen, R. Janssen, and J. Bakker. 1997. Mapping of the cyst nematode resistance locus *Gpa2* in potato using a strategy based on comigrating AFLP markers. Theor Appl Genet 95:874-880.

Rouppe van der Voort, J., W. Lindeman, R. Folkertsma, R. Hutten, H. Overmars, E. van der Vossen, E. Jacobsen, and J. Bakker. 1998. A QTL for broad-spectrum resistance to cyst nematode species (*Globodera* spp.) maps to a resistance gene cluster in potato. Theor Appl Genet 96:654-661.

Rouppe van der Voort, J.N.A.M., G.J.W. Janssen, H. Overmars, P.M. van Zandvoort, A. van Norel, O.E. Scholten, R. Janssen, and J. Bakker. 1999. Development of a PCR-based selection assay for root-knot nematode resistance (*Rmc1*) by a comparative analysis of the *Solanum bulbocastanum* and *S. tuberosum* genome. Euphytica 106:187-195.

Skroch, P., and J. Nienhuis. 1995. Impact of scoring error and reproducibility of RAPD data on RAPD based estimates of genetic distance. Theor Appl Genet 91:1086-1091.

Staub, J., J. Bacher, and K. Poetter. 1996. Sources of potential errors in the application of random amplified polymorphic DNAs in cucumber. HortSci 31:262-266.

Tanksley, S.D., M.W. Ganal, J.P. Prince, M.C. de Vicente, M.W. Bonierbale, P. Broun, T.M. Fulton, J.J.Giovannoni, S. Grandillo, G.B. Martin, R. Messeguer, J.C. Miller, L. Miller, A.H. Paterson, O. Pineda, M.S. Röder, R.A. Wing, W. Wu, and N.D. Young. 1992. High density molecular linkage maps of the tomato and potato genomes. Genetics 132:1141-1160.

van Eck, H.J., J. Rouppe van der Voort, J. Draaistra, P. van Zandvoort, E. van Enckevort, B. Segers, J. Peleman, E. Jacobsen, J. Helder, and J. Bakker. 1995. The inheritance and chromosomal localization of AFLP markers in a non-inbred potato offspring. Mol Breed 1:397-410.

Williams, J.G.K., A.R. Kubelik, K.J. Livak, J.A. Rafalski, and S.V. Tingey. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nucleic Acids Res 18:6531-6535.