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Identification of 2n breeding lines and 4n varieties of potato (*Solanum tuberosum*, ssp. *tuberosum*) with RFLP-fingerprints

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Summary. The possibility of genotype identification with RFLP fingerprints was examined with 20 tetraploid potato varieties and 38 diploid potato lines. By using a sensitive detection system for small restriction fragment length differences and highly variable potato sequences as probes, all genotypes (diploids and tetraploids) were distinguished by a minimum of two probe/enzyme combinations. The best single probe/enzyme combination distinguished 19 out of 20 4n varieties and 33 out of 38 2n lines. Intravarietal variability was very small compared to the intervarietal variability, and patterns obtained with different DNA sources of the same genotype were identical.

Key words: RFLP – Potato – Fingerprint – Variety identification

Introduction

The unequivocal identification of a genotype by DNA fingerprinting has been demonstrated in humans by Jeffreys et al. (1985a, 1985b). Even closely related individuals could be distinguished on the basis of their complex pattern of restriction fragments on Southern blots revealed by one or two hypervariable probes (minisatellites). In plants, genotype-specific RFLP patterns (RFLP = restriction fragment length polymorphism) would have applications in the identification of breeding lines and varieties as well as in the characterization of germplasm resources (Beckmann and Soller 1986).

RFLP-studies in maize (Evola et al. 1986; Helentjaris et al. 1985), oilseed (Figdore et al. 1988), lettuce (Landry et al. 1987), soybean (Apuya et al. 1988) and rice (McCouch et al. 1988) have shown that varieties can be distinguished from each other by RFLPs. Such polymorphisms have been widely used for the construction of linkage maps. An exception appears to be the tomato, in which intervarietal differences were rarely found (Helentjaris et al. 1985). Depending on the existing variability in each species, an increasing number of probe-enzyme combinations would have to be used in order to distinguish a large number of sometimes closely related varieties or lines. Probes equivalent in resolution to Jeffreys "minisatellites" have not been reported in plants.

The cultivated European potato, *Solanum tuberosum*, ssp. *tuberosum* originates from a few introductions from the Andean region of South America (Simmonds 1976). Despite its narrow genetic base, a high degree of polymorphism at the DNA level was detected within the subspecies (Gebhardt et al. 1989). Using highly polymorphic RFLP markers, together with a sensitive separation technique for restriction fragments based on four cutter restriction enzymes and denaturing polyacrylamide gels (Kreitman and Aquadé 1986), we could distinguish, with a minimum of two probe/enzyme combinations, 20 registered potato varieties as well as 38 diploid breeding lines.

Materials and methods

Diploid breeding lines

Thirty-eight diploid *Solanum tuberosum* lines from the collection of the Max-Planck-Institut für Züchtungsforschung (MPI) were used in this study. The line identifications, together with the running numbers, are listed in Table 1. For DNA extraction, leaves and young shoots were harvested from pot grown plants in the greenhouse, frozen in liquid nitrogen and stored at −70 °C until used.

Tetraploid varieties

Shoots of 20 registered varieties were harvested in August 1987 from plants growing in the field at Scharnhorst, the outstation

Table 1. List of 2n lines used

Line no.	Line identification [1]	Line no.	Line identification
3	H 80.577/1	30	H 82.350/7
5	H 80.649/1	31	H 75.1207/7
6	H 80.695/12	32	H 75.1208/13
7	H 81.8/1	33	H 76.7/7
9	H 81.691/1	34	H 77.409/13
10	H 81.2045/10	35	H 77.420/10
11	H 81.2062/1	37	H 80.572/5
12	H 81.2077/11	38	H 80.576/16
13	H 79.0134/44	39	H 79.0136/76
15	H 82.24/3	40	H 80.696/4
16	H 82.309/5	41	H 79.1506/1
17	H 82.310/4	44	H 81.404/89
18	H 82.337/49	45	H 82.310/10
19	H 82.340/18	46	H 82.355/7
20	H 82.350/6	47	H 82.364/19
23	H 82.379/7	48	H 82.366/3
27	H 81.802/7	49	H 82.368/3
28	H 81.2074/2	50	H 82.2032/1
29	H 82.328/13	51	H 81.1506/60

[1] The first two digits after the letter refer to the year of clone isolation

of the MPI. The varieties were Amigo, Assia, Aula, Bintje, Bodenkraft, Darwina, Datura, Granola, Hansa, Indira, Isola, Nena, Ponto, Quarta, Ragna, Roxy, Saturna, Sira, Taiga and Valetta. Freezing and storage was as for 2n lines. Tubers derived from seed tuber stock plants were provided by the breeders of the varieties Assia (Uniplanta-Saatzucht, Niederarnbach, FRG), Datura (D. von Kameke, Grabau, FRG) and Hansa (Vereinigte Saatzuchten, Ebstorf, FRG). DNA was extracted from peeled, freeze-dried tubers which were stored at −20 °C.

DNA from leaves and tubers was extracted according to Saghai-Maroof et al. (1984) and purified according to Gebhardt et al. (1989).

The genomic DNA (ca. 5 µg per gel sample) was digested with the restriction enzymes TaqI and RsaI, respectively, using 3 enzyme units per µg DNA for 4 h or overnight, according to the supplier's instructions (Boehringer, Mannheim).

The restriction fragments were size-separated on a denaturing 4% polyacrylamide gel and electrophoretically transferred onto a nylon membrane (Amersham, Hybond N), as described by Gebhardt et al. (1989).

The inserts of two random genomic potato clones (GP1 and GP26, 870 bp and 940 bp, respectively) and one random potato cDNA-clone (CP6, 460 bp) were used as probes (Gebhardt et al. 1989). The inserts were labelled to high specific activities with the random primer method of Feinberg and Vogelstein (1983, 1984) using α-(^{32}P)-dCTP as the radioactive nucleotide (Amersham). Prehybridization, hybridization, posthybridization washes and auto-radiography were performed as described elsewhere (Gebhardt et al. 1989).

Clearly identifiable restriction fragments of each probe/enzyme combination were individually numbered. The presence or absence of each fragment was scored with 1 and 0, respectively in the 2n lines and 4n varieties. Those cases in which presence or absence of a fragment was questionable were scored with −1. The matrix tables (genotypes × fragments) containing the values 1, 0 or −1 were computed using the programme package WORDS & FIGURES (Lifetree Software). Data analysis was performed with an IBM-compatible PC and software developed by E. Ritter (unpublished results).

Results

During a search for RFLP markers suitable for linkage analysis in diploid potatoes (Gebhardt et al. 1989), probes were encountered which showed highly variable, although well-spaced, fragment patterns on genomic Southern blots within a set of 38 diploid potato lines. The question was addressed as to whether such "hypervariable" sequences could also be used for the identification of tetraploid potato varieties. Twenty registered varieties were selected ranging from Bintje (first registered 1910), as an old pure *tuberosum* type variety, to modern varieties such as Assia (1980) or Valetta (1984), in which germplasm from several wild *Solanum* species was incorporated (Stegemann and Schnick 1985).

Total genomic DNA was isolated from 2n lines and 4n varieties and restricted with TaqI and RsaI respectively. The fragments were size-separated on a denaturing 4% polyacrylamide gel and transferred to a nylon membrane by electroblotting. The filters were hybridized in turn against the labelled inserts of the two random genomic clones, GP1 and GP26, and the anonymous cDNA clone CP6.

Comparison of 2n lines and 4n varieties

The fragment pattern for one out of six probe/enzyme combinations, GP1/TaqI, is shown in Fig. 1 A for 2n lines and in Fig. 1 B for 4n varieties. Out of 40 scored fragments in both populations, 38 were polymorphic (fragments 1–38 and 2 were homomorphic (fragments H1 and H2). Fragments were considered only if their presence or absence could be assessed in most lines of each set. Twenty-seven fragments were common to both 2n and 4n populations, 10 being polymorphic only in the 2n lines and homomorphic in the varieties (fragments 8, 10, 12, 16, 20, 22, 24, 27, 28, 38), indicating that the varieties were more uniform with this probe compared to the diploid lines. Polymorphic fragments, present either in 2n lines or 4n varieties, were also detected (fragments 13, 19 and 32, 36, 37, respectively). However, they occurred in low frequencies or were weakly hybridizing fragments. The patterns of all six probe/enzyme combinations were analysed in a similar way, as demonstrated for GP1/TaqI, for common, 2n and 4n specific fragments, considering only polymorphic and homomorphic fragments scorable in both sets. The result is shown in Table 2. Ninety-four out of 111 scored fragments (85%) were present in both populations, 10 (9%) were detected only in diploids and 7 (6%) only in tetraploids. None of the specific fragments were very frequent or strongly hybridizing.

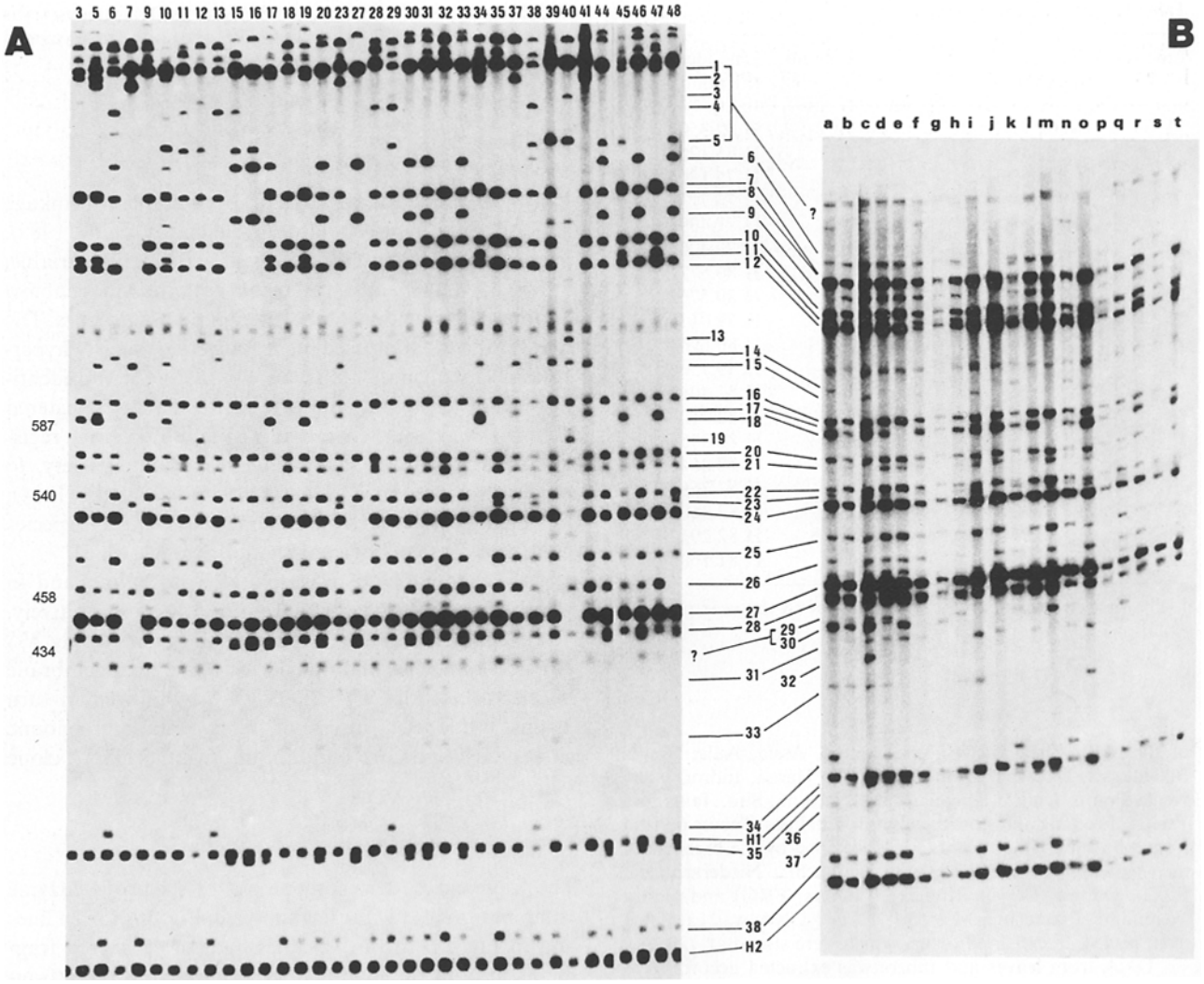

Fig. 1 A and B. Southern blot of 2n lines **A** and 4n varieties **B**. Total DNA was restricted with TaqI. Restriction fragments were separated on a denaturing 4% polyacrylamide gel, transferred to a Nylon membrane and hybridized to the random genomic sequence GP1. Fragments common to both sets, present either in 2n lines or 4n varieties, and fragments with uncertain identification are indicated between **A** and **B.** Molecular weight markers are indicated on the left hand side of **A. A** For the identification of 2n lines, see Table 1. **B** *a* – Granola, *b* – Valetta, *c* – Darwina, *d* – Roxy, *e* – Indira, *f* – Bintje, *g* – Hansa, *h* – Taiga, *i* – Bodenkraft, *j* – Datura, *k* – Amigo, *l* – Quarta, *m* – Nena, *n* – Ponto, *o* – Isola, *p* – Saturna, *q* – Assia, *r* – Aula, *s* – Sira, *t* – Ragna

Table 2. Fragment distribution in 2n lines and 4n varieties

	Total no. considered	Common to 2n and 4n	2n specific	4n specific
GP1/TaqI	32	27	2	3
GP1/RsaI	21	20	1	0
CP6/TaqI	18	16	1	1
CP6/RsaI	14	12	2	0
GP26/TaqI	11	10	0	1
GP26/RsaI	15	9	4	2
Total	111	94	10	7
%	100%	85%	9%	6%

The criterion for choosing the set of 38 diploid lines was their heterogeneity in morphological and agronomical traits. Hybrids between *S. tuberosum* and wild *Solanum* species (lines 6 and 40) were included, as well as largely pure *tuberosum* line (e.g. line 13, see also Gebhardt et al. 1989). The population of diploids, therefore, represented an apparently wider gene pool than the group of varieties. Nevertheless, the high percentage of common fragments suggested that the two populations were fairly good representatives of the species *Solanum tuberosum*.

The number of fragments present in an individual line, compared to the number of all fragments scored in

the population was positively correlated with the relative heterozygosity of that line within the population (Gebhardt et al. 1989). Relative heterozygosity indices (RHI) were calculated for the 2n and 4n lines, taking into account the fragments of the three probes separately as well as all fragments combined (RHI = number of fragments per line divided by number of fragments scored in the population). The mean RHI values are shown in Table 3. As expected, the tetraploid varieties had higher heterozygosity indices than the diploid lines.

Number of patterns

The individual polymorphic fragments in the six probe/enzyme combinations were scored for presence or absence ('Materials and methods') in the 38 2n lines and 20 4n varieties. From these data the number of different patterns was determined, resulting from the six single probe/enzyme combinations, the 15 possible double combinations and 2 of 60 possible triple combinations. In addition, the number of fragments by which any pair of diploid and tetraploid lines respectively differed from each other was calculated (703 pairwise comparisons for the 38 diploids and 190 for the 20 tetraploids).

Table 4 summarizes the results of the computer analysis. No single probe/enzyme combination was sufficient in distinguishing all 38 diploid lines and all 20 varieties. However, the combination of probe GP1 with the enzyme TaqI (Fig. 1) came very close by revealing 19 out of 20 and 33 out of 38 possible patterns. From the 15 double and 2 triple combinations, all but 3 distinguished the 20 varieties (indicated by * in Table 4), 6 distinguished the 38 diploids and 5 could differentiate all, diploids as well as tetraploids (GP1/Taq + GP26/Taq, GP1/Rsa + CP6/Taq, GP1/Rsa + GP26/Taq, GP1/Rsa + GP26/Rsa and GP1/Taq + CP6/Taq + GP26/Taq).

In the diploid set, lines closely related by pedigree, such as pairs of full sib lines, differed not only in the indicated most effective combinations but also with single probe/enzyme combinations: sister lines 20 and 30 with GP1 and CP6 (either enzyme, 1–3 fragments) and

Table 3. Relative heterozygosity index (RHI) in diploids and tetraploids (standard deviation)

	2n	4n
GP1	0.47 (0.08)	0.62 (0.06)
CP6	0.28 (0.08)	0.50 (0.12)
GP26	0.15 (0.07)	0.34 (0.07)
GP1 CP6 GP26	0.36 (0.06)	0.52 (0.05)

Table 4. Pattern comparison of 4n varieties and 2n breeding lines

Probe/enzyme combination	No. of fragments	No. of patterns		Min-max no. of differing fragments		Mean no. of differing fragments (StD)	
		4n	2n	4n	2n	4n	2n
GP1/Taq	38	19	33	0–14	0–21	7.2 (1.0)	9.0 (2.5)
GP1/Rsa	20	18	34	0–9	0–14	4.4 (0.8)	5.6 (1.7)
CP6/Taq	18	15	24	0–14	0–14	5.2 (1.5)	5.7 (1.1)
CP6/Rsa	13	12	17	0–9	0–10	3.9 (0.9)	3.2 (1.5)
GP26/Taq	11	16	16	0–9	0–7	3.4 (0.7)	2.9 (0.7)
GP26/Rsa	15	17	12	0–7	0–9	3.4 (0.5)	2.6 (1.0)
GP1/Taq + GP1/Rsa	58	19	38*	0–21	1–35	11.5 (1.5)	14.6 (3.9)
GP1/Taq + CP6/Taq	56	20*	36	3–26	0–30	12.4 (2.1)	14.7 (3.1)
GP1/Taq + CP6/Rsa	51	20*	34	2–21	0–29	11.1 (1.4)	12.3 (3.4)
GP1/Taq + GP26/Taq	49	20*	38*	4–20	1–27	10.6 (1.3)	12.0 (2.6)
GP1/Taq + GP26/Rsa	53	20*	37	4–18	0–28	10.6 (1.1)	11.6 (2.8)
GP1/Rsa + CP6/Taq	38	20*	38*	1–20	1–23	9.6 (1.9)	11.2 (2.0)
GP1/Rsa + CP6/Rsa	33	20*	37	1–18	0–21	8.3 (1.1)	8.8 (2.5)
GP1/Rsa + GP26/Taq	31	20*	38*	2–15	1–19	7.8 (1.1)	8.5 (1.8)
GP1/Rsa + GP26/Rsa	35	20*	38*	1–14	1–20	7.7 (0.8)	8.2 (2.0)
CP6/Taq + Cp6/Rsa	31	17	26	0–20	0–21	9.1 (1.9)	8.9 (2.2)
CP6/Taq + GP26/Taq	29	20*	35	1–20	0–19	8.7 (1.7)	8.6 (1.2)
CP6/Taq + GP26/Rsa	33	20*	34	1–18	0–19	8.6 (1.5)	8.3 (1.5)
CP6/Rsa + GP26/Taq	24	20*	28	1–15	0–16	7.4 (1.3)	6.0 (1.7)
CP6/Rsa + GP26/Rsa	28	20*	25	2–14	0–15	7.3 (1.0)	5.7 (1.9)
GP26/Taq + GP26/Rsa	26	18	17	0–16	0–16	6.8 (1.1)	5.5 (1.7)
GP1/Taq + CP6/Taq + GP26/Taq	67	20*	38*	5–33	1–34	15.8 (2.3)	17.6 (3.2)
GP1/Taq + CP6/Taq + GP26/Rsa	71	20*	37	4–31	0–35	15.8 (2.0)	17.3 (3.4)

* see text

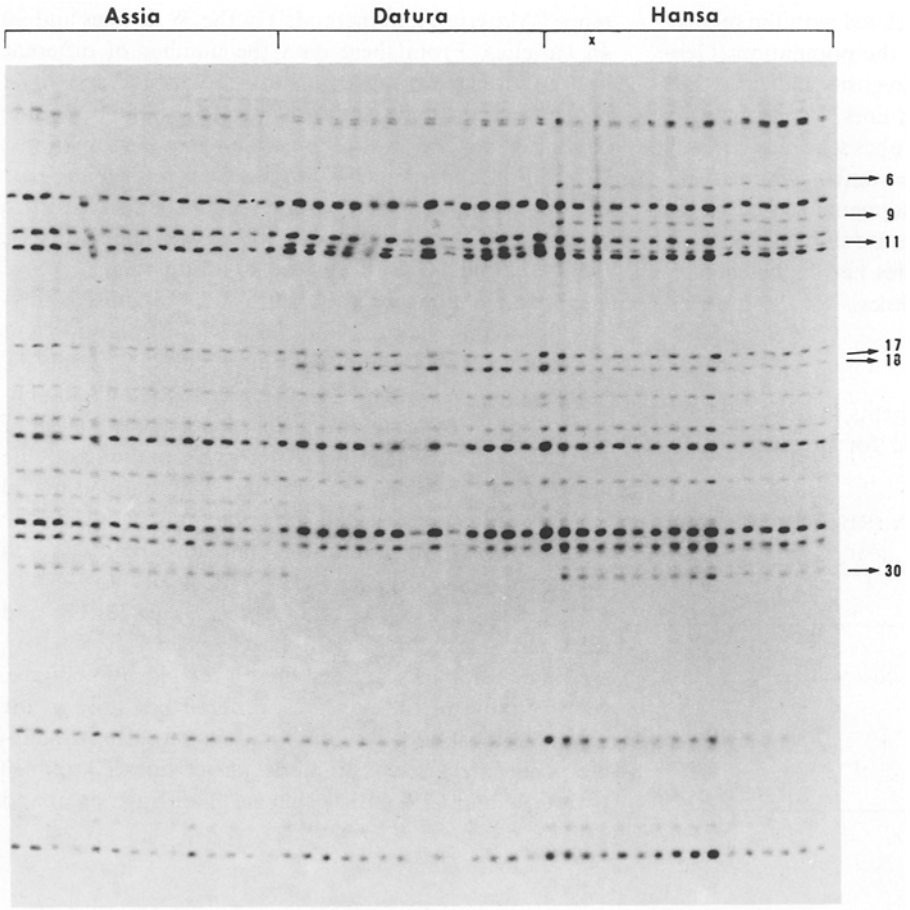

Fig. 2. Southern blot with DNA from 15 tubers each of the three varieties Assia, Datura and Hansa, restricted with TaqI and hybridized to GP1 as in Fig. 1. The fragments distinguishing the 3 varieties are indicated with the same numbers as in Fig. 1. The possible exception in the Hansa-series is marked with an X

sister lines 17 and 45 with GP1 and GP26 (either enzyme, 2–7 fragments).

The higher the number of fragments in which two genotypes differ, the more reliable would be the distinction between them. Therefore, those probe/enzyme combinations providing more than one fragment as the minimum difference would better describe genotypic differences. The mean numbers of differing fragments (calculated from all pairwise comparisons) as well as their minimum-maximum range indicated that – whenever a difference between genotypes was noted – in most cases it could be determined safely, based on several restriction fragments (Table 4). Six of the double probe/enzyme combinations offered at least 2 fragments for the minimum difference between any of the 20 varieties.

Despite the higher heterozygosity of the varieties (Table 3), it was also evident that the number of fragments differing in the comparisons between two varieties was similar or sometimes even lower than between two diploid lines (Table 4).

Controls

To test the reproducibility of the RFLP pattern, the same experiments as for the diploid lines and varieties were performed with DNA extracted from 15 tubers each of the three varieties Assia, Datura and Hansa. The tubers were obtained from the breeder of the variety and originated from 15 different plants. The same probe/enzyme combination, GP1/TaqI, as in Fig. 1 is shown in Fig. 2. Within the varieties the patterns were identical, with only one exception in the Hansa series (indicated in Fig. 2), where one faint additional fragment appeared. The possibility of an artifact or of a partially digested fragment cannot be excluded. A discrepancy between the patterns obtained with leaf DNA of an independent source and the tuber DNA was not observed. In contrast, the "fingerprints" of the three varieties were clearly different from each other.

Discussion

According to Bailey (1983), the basic criteria to be fulfilled by a character used for variety identification are: (1) distinguishable intervarietal variation, (2) minimal intravarietal variation, (3) environmental stability, and (4) in case of biochemical or molecular characters, experimental reproducibility. The results reported in this paper

show that, with molecular probes, DNA-fingerprints of potato genotypes can be obtained which satisfy all the criteria mentioned above.

Intervarietal variation

With several combinations of three probes and two restriction enzymes, 38 diploid (including full sib lines) and 20 tetraploid potato genotypes were clearly distinguishable from each other. Sufficient were double combinations of two probes and one or two enzymes. The best single probe/enzyme combination was able to discriminate among 19 varieties and 33 diploid lines (GP1/TaqI).

Isozymes and tuber sap proteins have been used to identify potato 4n varieties (Zwartz 1966; Desborough and Peloquin 1968; Stegemann and Loeschke 1977; Stegemann et al. 1973; Stegemann and Schnick 1985). The most elaborate system characterizes 629 European potato varieties by a combination of tuber protein patterns and esterases (Stegemann and Schnick 1985; Stegemann and Loeschke 1976). Because of the limited population size of 20 varieties, it was not possible to determine the maximum potential for variety identification of the three RFLP probes used in this study. By segregation analysis, only one genetic locus was identified for both CP6 and GP26 and four for GP1, although most segregating fragments revealed by this probe were also accounted for by a single locus (Gebhardt et al. 1989). GP1 and GP6, but not GP26, showed additional non-segregating fragments which could either be homomorphic constituents of the segregating alleles or account for further genetic loci not segregating in the specific backcross. This is unlike Jeffreys' hypervariable minisatellite probes (Jeffreys et al. 1985a), which detected several unlinked loci. Fragment linkage reduces the potential variability compared to independently segregating fragments. The observed variability with double combinations of GP1, CP6, GP26 and the restriction enzymes TaqI and RsaI might, therefore, not be sufficient to distinguish all 629 potato varieties. However, the increased heterozygosity of the varieties should enhance the potential of each single probe.

In addition, we stress that the three probes considered here are not exceptional in detecting polymorphism between potato genotypes. From ca. 150 analysed potato sequences, 20 were able to distinguish half or more of the 38 diploid lines with a single probe/enzyme combination, and one probe could distinguish all (Gebhardt et al. 1989). The variability seems, therefore, more a consequence of the experimental technique than of the use of a rare and specific type of sequence. Combining the right probes with the right enzymes, most potato varieties may in any case be "fingerprinted" using only a few probes.

Intravarietal variation

Because the cultivated potato is vegetatively propagated, each potato variety should have a very stable genotype. Changes should occur only as a result of somatic mutations or of genotype mix-up caused by incorrect handling. The control experiment (Fig. 2) showed, in a sample size of 15 tubers for each of three varieties, that there is no significant intravarietal variation compared to the intervarietal differences. The DNAs used in the control experiments and in the variety comparison originate from different tissues (leaves and tubers) and from two independent breeding sources. The patterns observed were identical. The three varieties were chosen according to their age. Hansa and Datura were both first registered in 1957, and Assia in 1980. The time of propagation did not seem to increase intravarietal variation, at least not within the limits of this study.

Environmental stability

Fingerprints based on RFLPs, by definition, should be independent from the influence of the environment. This is an advantage over variety identification by isozyme or protein patterns, which is limited by the stability of the pattern in a specific tissue (Stegemann et al. 1973).

Experimental reproducibility

The RFLP patterns were reproducible, including minor fragments, as shown by identical patterns from different DNA sources and different experiments. The patterns were not sensitive to minor changes in experimental parameters, because fragments were identified rather by their relative position to other fragments than by their absolute position (compare Fig. 1 A and B).

In conclusion, RFLP fingerprints of high resolution and reproducibility were obtained for potato genotypes using a sensitive experimental system and molecular probes of above average variability. For practical purposes, the use of radioactive probes and the comparatively expensive and, at present, labour-intensive technology are disadvantages. However, with already commercially available methods for nonradioactive labelling and with standardization and partial automatization of the techniques involved, the RFLP-fingerprint technology might be developed into a valuable and reliable varietal diagnostic tool.

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References

Apuya NR, Frazier BL, Keim P, Roth EJ, Lark KG (1988) Restriction fragment length polymorphisms as genetic markers in soybean, *Glycine max* (L.) merrill. Theor Appl Genet 75:889–901

Bailey DC (1983) Isozymic variation and plant breeder's rights. In: Tanksley SD, Orton TJ (eds) Isozymes in plant genetics and breeding, part A. Elsevier, Amsterdam, pp 425–440

Beckmann JS, Soller M (1986) Restriction fragment length polymorphisms and genetic improvement of agricultural species. Euphytica 35:111–124

Desborough S, Peloquin SJ (1968) Potato variety identification by use of electrophoretic patterns of tuber proteins and enzymes. Am Potato J 45:220–229

Evola SV, Burr FA, Burr B (1986) The suitability of restriction fragment length polymorphisms as genetic markers in maize. Theor Appl Genet 71:765–771

Feinberg AP, Vogelstein B (1983) A technique for radiolabeling DNA restriction endonuclease fragments to high specific activity. Anal Biochem 132:6–13

Feinberg AP, Vogelstein B (1984) A technique for radiolabeling DNA restriction endonuclease fragments to high specific activity. Addendum. Anal Biochem 137:266–267

Figdore SS, Kennard WC, Song KM, Slocum MK, Osborn TC (1988) Assessment of the degree of restriction fragment length polymorphism in *Brassica*. Theor Appl Genet 75: 833–840

Gebhardt C, Ritter E, Debener T, Schachtschabel U, Walkemeier B, Uhrig H, Salamini F (1989) RFLP analysis and linkage mapping in *Solanum tuberosum*. Theor Appl Genet (in press)

Helentjaris T, King G, Slocum M, Siedenstrang C, Wegman S (1985) Restriction fragment polymorphisms as probes for plant diversity, and their development as tools for applied plant breeding. Plant Mol Biol 5:109–118

Jeffreys AJ, Wilson V, Thein SL (1985a) Hypervariable "minisatellite" regions in human DNA. Nature 314:67–73

Jeffreys AJ, Wilson V, Thein SL (1985b) Individual-specific "fingerprints" of human DNA. Nature 316:76–79

Kreitman M, Aquadé M (1986) Genetic uniformity in two populations of *Drosophila melanogaster* as revealed by four-cutter filter hybridization. Proc Natl Acad Sci USA 83: 3562–3566

Landry BS, Kesseli R, Hei Leung, Michelmore RW (1987) Comparison of restriction endonucleases and sources of probes for their efficiency in detecting restriction fragment length polymorphisms in lettuce (*Lactuca sativa* L.). Theor Appl Genet 74:646–653

McCouch SR, Kochert G, Yu ZH, Wang ZY, Khush GS, Coffman WR, Tanksley SD (1988) Molecular mapping of rice chromosomes. Theor Appl Genet 76:815–829

Saghai-Maroof MA, Soliman KM, Jorgensen RA, Allard RW (1984) Ribosomal DNA spacer-length polymorphisms in barley: Mendelian inheritance chromosomal location and population dynamics. Proc Natl Acad Sci USA 81: 8014–8018

Simmonds NW (1976) Potatoes. In: Simmonds NW (ed) Evolution of crop plants. Longman, London New York, pp 279–283

Stegemann H, Loeschke V (1976) Index of European potato varieties. Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft, Heft 168. Parey, Berlin Hamburg

Stegemann H, Loeschke V (1977) Das europäische Kartoffelsortiment und seine Indexierung. Potato Res 20:101–110

Stegemann H, Schnick D (1985) Index 1985 of European potato varieties. Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft, Heft 227. Parey, Berlin Hamburg

Stegemann H, Francksen H, Macko V (1973) Potato proteins: genetic and physiological changes, evaluated by one- and two-dimensional PAA-gel-techniques. Z Naturforsch 28: 722–732

Zwartz JA (1966) Potato varieties and their protein electropherogram characteristics. Eur Potato J 9:111–128