Microsatellite marker analysis of an anther-derived potato family: skewed segregation and gene–centromere mapping

Eduard Chani, Varda Ashkenazi, Jossi Hillel, and Richard E. Veilleux

Abstract: Segregation patterns of polymorphic simple sequence repeat (SSR) primer pairs were investigated in monoploid potato families derived from anther culture. A total of 14 primers developed from the sequences in the database, as well as from a genomic library of potato, was used. Distorted segregation was observed for seven (50%) polymorphic loci among monoploids derived from an interspecific hybrid. Similar distortion was observed for only one of five loci that could be contrasted between the two monoploid families. Segregation distortion was less common in the sexually derived backcross population between the interspecific hybrid and either of its parents. One locus could be putatively linked to a lethal allele because it showed distorted segregation in both monoploid families, a group of 70 heterozygous diploids derived from unreduced gametes through anther culture, and a backcross population. These diploids were used to map the polymorphic SSR markers with respect to the centromeres using half-tetrad analysis. The majority of the SSR loci mapped more than 33 cM from the centromere, suggesting the occurrence of a single crossover per chromosome arm.

Key words: androgenesis, segregation distortion, simple sequence repeats (SSRs), Solanum phureja, unreduced gametes.

Introduction

An anther-derived plant population generally represents a minute fraction of male gametes that have survived the rigors of selection in two tissue culture operations; specifically, androgenic embryo formation and subsequent embryo conversion. It has been debated as to whether or not this population represents a similar array of genotypes expected from sexual crosses, with contrasting results. Bjornstad et al. (1993) found that wheat (Triticum aestivum L.) lines derived from single-seed descent exhibited a frequency of skewed segregation for marker genes similar to that of anther-derived doubled haploid lines. However, greater frequencies of distorted loci have been found in anther-derived populations of rice (Oryza sativa L.; Xu et al. 1997), barley (Hordeum vulgare L.; Graner et al. 1991), and the weedy potato species Solanum chacoense Bitt. (Rivard et al. 1996). When one parent of a hybrid used to construct an anther-derived mapping population has been known to respond more readily to anther culture, distortion with an excess of alleles from the more responsive parent has been found in maize (Zea mays L.; Murigneux et al. 1993a) and barley (Graner et al. 1991).

Simple sequence repeats (SSRs), otherwise known as microsatellites, have been found to occur abundantly in plant genomes (Wang et al. 1994; Cardle et al. 2000). Several studies have been published documenting their occurrence in the potato genome (Veilleux et al. 1995; Provan et al. 1996a;
Milbourne et al. 1998; Ashkenazi et al. 2001). They have been applied to the genetic study of potato in various aspects, such as DNA fingerprinting to distinguish cultivars (Kawchuk et al. 1996; Provan et al. 1996b; 1999; Schneider and Douches 1997; Milbourne et al. 1997; McGregor et al. 2000) or species (Bryan et al. 1999; Ashkenazi et al. 2001). Similarly, somatic hybrids have been distinguished from parental somaclones (Provan et al. 1996c; Matthews et al. 1999; Johnson et al. 2001). Veilleux et al. (1995) and Chani et al. (2000) used SSR polymorphism to distinguish homzygous doubled monoploid from heterozygous anther-derived diploid plants. Finally, Chulow and Rousselle-Bourgeois (1997) documented introgression of microsatellite markers from a haploid-inducing pollinator into dihaploids extracted from tetraploid potato cultivars.

Genetic maps of potato have been constructed (Bonierbale et al. 1988; Gebhardt et al. 1991; Tanksley et al. 1992; Jacobs and Teng 1995) using morphological and molecular markers. Although the maps are relatively dense with marker loci, the positions of the centromeres in relation to the mapped loci are not precisely indicated (Bastiaanssen et al. 1996). Gene–centromere mapping by half-tetrad analysis (HTA) has been used successfully in potato using 4x × 2x crosses (Mendiburu and Peloquin 1979; Douches and Quiros 1987; Bastiaanssen et al. 1996). In these studies, morphological, as well as isozyme, loci have been mapped with respect to their centromeres. In the study reported here, an attempt to map SSR loci with respect to centromeres is made for the first time using segregation data from unreduced gametes. The objectives of this study were as follows: (i) to characterize the segregation pattern of polymorphic SSR loci in a monoploid anther-derived population and (ii) to map polymorphic SSR loci with respect to the centromere using HTA.

Materials and methods

Plant material and DNA extraction

The anther-derived CP2 family developed in a previous study (Chani et al. 2000) was used to analyze segregation patterns of SSR markers. It included 32 monopoloids and 14 homzygous diploids obtained through anther culture of an

Molecular analysis

Total genomic DNA was extracted from in vitro plant material according to Doyle and Doyle (1987). Fourteen SSR primer pairs that revealed polymorphism between BARD 1-3 and chc 80-1 according to Ashkenazi et al. (2001) were used on the anther-derived and backcross populations. Of these 14 primer pairs, 10 were developed from sequences of potato genes in the public databases, 3 were developed from a potato genomic library, and 1 was from a tomato genomic library (Table 1). Amplification reactions were based on the procedure reported by Yu et al. (1994). The reaction mixture (20 μL) contained the following: 1x assay buffer (50 mM KCl, 10 mM Tris-HCl (pH 9), 1% Triton X-100), 3 mM MgCl2, 160 μM of each dNTP, 1.5 U Taq polymerase (Promega, Madison, Wis.), and 0.1 μM of each primer. Genomic DNA template (50 ng) was added and the reaction mixture was covered by a drop of mineral oil. A second reaction mixture was used for those primers (31 + 32, 57 + 58, and tom 8 + 9) developed from the genomic library. The total volume of this mixture was 10 μL and contained 0.15 μM primer, 2.5 mM MgCl2, 100 μM of each dNTP, 1x assay buffer, 1 U Taq polymerase, and 30 ng DNA template. A typical PCR protocol consisting of 40 cycles at 94°C for 1 min, 55°C for 2 min, 72°C for 1.5 min, followed by 5 min at 72°C was used; for primer pairs that gave strong amplification signals the number of cycles was reduced to 30. Amplified fragments were separated in 3% Metaphor agarose gels (FMC Bioproducts, Rockland, Maine) in Tris-borate–EDTA buffer for 4 h at 90–100 V (Sambrook et al. 1989). Alternatively, for shorter repeats, amplification products were run in polyacrylamide gels using an ABI 377 DNA sequencer (Applied Biosystems, Foster City, Calif.) according to the manufacturer’s instructions. The results were analyzed by GeneScan (Applied Biosystems) and the precise size of the SSR was determined for each individual.

Segregation analysis

Segregation ratios (in the CP2 monoploid family) were calculated for all primer pairs. We performed χ² tests to check for the distorted segregation of alleles for each primer pair. For microsatellites that showed skewed segregation ratios in the CP2 monoploid family, the analysis was extended to one of the backcross families (CP2 × chc 80-1 or BARD 1-3 × CP2) and to the anther-derived BARD 1-3 monoploid family (30, 32, and 31 individuals per family, respectively). Pairwise χ² tests were conducted in the CP2 monoploid population for markers that exhibited normal segregation to determine linkage. The partially heterozygous anther-derived plants were used to determine linkage for those markers that exhibited distorted segregation in the CP2 monoploid family and data obtained were used to determine gene–centromere map distances (Douches and Quiros 1987).

Results

All 14 polymorphic primer pairs exhibited specific alleles in each of the parents, and CP2 inherited one allele each from chc 80-1 and BARD 1-3. Half of the polymorphic loci exhibited distorted segregation in the CP2 monoploid family (Table 1). Distortion ranged from complete absence of the chc allele for the SSR amplified by primers 31 + 32 to complete absence of the phi allele for the SSR amplified by primers 11 + 12. Under-representation of the chc allele characterized two additional SSRs amplified by primers 23 + 24 and 67 + 68, whereas under-representation of the phi allele characterized three additional SSRs amplified by primers 3 + 4

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For markers showing distorted segregation in the CP2 monoploids, the analysis was extended to either the anther-derived monoploids of BARD 1-3 or one of the backcross families (CP2 × chc80-1 and BARD 1-3 × CP2).

Not all of the markers that were polymorphic in the CP2 monoploid family were similarly polymorphic in the BARD 1-3 monoploid family. Hence, only some of the same loci could be analyzed in this family. Two of the SSRs with under-representation of the phu allele (amplified by primers 3 + 4 and 5 + 6) in the CP2 monoploid family exhibited normal segregation in the BARD 1-3 family. However, the GAA repeat within the starch phosphorylase gene, amplified by primer pair 11 + 12, exhibited the same extreme distortion in both families. This locus was skewed towards the chc (A) allele even in one of the backcross populations (Table 2; Fig. 2). One locus (amplified by primers 21 + 22) that was distorted in the BARD 1-3 monoploid family by over-representation of the A allele appeared to segregate normally in the CP2 monoploid family. However, there were many more individuals with the A allele even in the CP2 monoploid family, such that a larger population size may have revealed similar distortion in both families.

Segregation distortion was generally less in the backcross families. Only two loci exhibited distorted segregation in these families: the one amplified by primers 11 + 12 (mentioned above) and the STLS1 locus, amplified by primer pair 23 + 24. This locus showed segregation distortion in favor of

### Table 1. Segregation ratios for SSR alleles among monoploids derived from an interspecific diploid potato hybrid (CP2), in backcross populations between CP2 and either of its parents (chc 80-1, BARD 1-3) and among BARD 1-3 monoploids.

<table>
<thead>
<tr>
<th>Primer pair</th>
<th>Locus</th>
<th>CP2 monoploids</th>
<th>CP2 × chc 80-1</th>
<th>BARD 1-3 × chc</th>
<th>BARD 1-3 × CP2</th>
</tr>
</thead>
<tbody>
<tr>
<td>3+4</td>
<td>STGBSS</td>
<td>35 6 20.51**</td>
<td>17 13 0.53</td>
<td>13 18 0.81 NS</td>
<td>7:5:12:8 3.25 NS</td>
</tr>
<tr>
<td>5+6</td>
<td>STPROINI</td>
<td>27 14 4.12*</td>
<td>25 5 13.33**</td>
<td>16 13 0.31 NS</td>
<td>6:22:4 4.75 NS</td>
</tr>
<tr>
<td>11+12</td>
<td>STSTP</td>
<td>41 0 41**</td>
<td>12 14 0.15 NS</td>
<td>31 0 31**</td>
<td>1:2:1:1 1.2 NS</td>
</tr>
<tr>
<td>15+16</td>
<td>STACCAS3</td>
<td>16 23 1.26NS</td>
<td>14 11 0.36 NS</td>
<td>6:22:4 4.75 NS</td>
<td></td>
</tr>
<tr>
<td>17+18</td>
<td>STWIN12G</td>
<td>23 12 3.46NS</td>
<td>22 9 5.45*</td>
<td>1:2:1:1 1.2 NS</td>
<td></td>
</tr>
<tr>
<td>19+20</td>
<td>POMT1-2</td>
<td>14 21 1.44NS</td>
<td>16 23 20.51**</td>
<td>5:10:8:8 1.63 NS</td>
<td></td>
</tr>
<tr>
<td>21+22</td>
<td>ST13ST def 4</td>
<td>23 13 2.78NS</td>
<td>20 6 7.54**</td>
<td>5:10:8:8 1.63 NS</td>
<td></td>
</tr>
<tr>
<td>23+24</td>
<td>STLS1</td>
<td>6 35 20.51**</td>
<td>22 9 5.45*</td>
<td>5:10:8:8 1.63 NS</td>
<td></td>
</tr>
<tr>
<td>31+32</td>
<td>Gen lib</td>
<td>0 37 37**</td>
<td>22 9 5.45*</td>
<td>5:10:8:8 1.63 NS</td>
<td></td>
</tr>
<tr>
<td>39+40</td>
<td>SCS10LP</td>
<td>32 6 17.79**</td>
<td>12 18 1.2 NS</td>
<td>2 5 1.28 NS</td>
<td>6:22:4 4.75 NS</td>
</tr>
<tr>
<td>57+58</td>
<td>Gen lib</td>
<td>23 18 0.61NS</td>
<td>12 18 1.2 NS</td>
<td>2 5 1.28 NS</td>
<td>6:22:4 4.75 NS</td>
</tr>
<tr>
<td>67+68</td>
<td>STCPKIN3</td>
<td>1 38 35.1**</td>
<td>5 6 0.1 NS</td>
<td>2 5 1.28 NS</td>
<td>6:22:4 4.75 NS</td>
</tr>
<tr>
<td>69+70</td>
<td>STGLGPB</td>
<td>19 23 0.38NS</td>
<td>5 6 0.1 NS</td>
<td>2 5 1.28 NS</td>
<td>6:22:4 4.75 NS</td>
</tr>
<tr>
<td>Tom 8+9 Gen lib</td>
<td>11 11 0 NS</td>
<td>2 5 1.28 NS</td>
<td>6:22:4 4.75 NS</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

For primer pairs 3 + 6, 19 + 20, and 21 + 22 the segregation patterns were complex because both CP2 and chc80-1 are heterozygous at these loci; however, no segregation distortion of individual alleles was observed.

BARD1-3 monoploids were not checked at loci 15 + 16, 19 + 20, 23 + 24, 39 + 40, 67 + 68, or tom 8 + 9 because BARD1-3 (the anther donor) was found to be homozygous; therefore, no segregation was expected.

For BARD 1-3 × CP2 the expected ratios were as follows: 3 + 4, 1:1:1:1; 11 + 12, 1:2:1; 31 + 32, 1:1:1:1; 39 + 40, 1:1; 67 + 68, 1:2:1.

a A, chc 80-1 allele; B, BARD 1-3 allele.

b Deviation from the expected segregation ratio. NS, not significant; * significant at 0.05% level; ** significant at 0.01% level.

Fig. 1. Distorted segregation of the waxy locus (STGBSS), amplified by primer pair 3 + 4, favoring the chc 80-1 allele in the anther-derived monoploid CP2 family. Lanes from left to right: (1) 100-bp λ DNA ladder; (2) chc 80-1; (3) BARD 1-3; (4) CP2; (5–30) 26 anther-derived monoploids of CP2.

(Fig. 1), 5 + 6, and 39 + 40. For markers showing distorted segregation in the CP2 monoploids, the analysis was extended to either the anther-derived monoploids of BARD 1-3 or one of the backcross families (CP2 × chc 80-1 and BARD 1-3 × CP2).

Not all of the markers that were polymorphic in the CP2 monoploid family were similarly polymorphic in the BARD 1-3 monoploid family. Hence, only some of the same loci could be analyzed in this family. Two of the SSRs with under-representation of the phu allele (amplified by primers 3 + 4 and 5 + 6) in the CP2 monoploid family exhibited normal segregation in the BARD 1-3 family. However, the GAA repeat within the starch phosphorylase gene, amplified by primer pair 11 + 12, exhibited the same extreme distortion in both families. This locus was skewed towards the chc (A) allele even in one of the backcross populations (Table 2; Fig. 2). One locus (amplified by primers 21 + 22) that was distorted in the BARD 1-3 monoploid family by over-representation of the A allele appeared to segregate normally in the CP2 monoploid family. However, there were many more individuals with the A allele even in the CP2 monoploid family, such that a larger population size may have revealed similar distortion in both families.

Segregation distortion was generally less in the backcross families. Only two loci exhibited distorted segregation in these families: the one amplified by primers 11 + 12 (mentioned above) and the STLS1 locus, amplified by primer pair 23 + 24. This locus showed segregation distortion in favor of
the *phu* allele in the CP2 monoploid family, but in favor of the *chc* allele in the backcross (CP2 × *chc* 80-1). Neither of the other loci (31 + 32 and 67 + 68) where the *phu* allele was favored in the CP2 monoploids exhibited distorted segregation in the BARD 1-3 × CP2 backcross.

### Linkage analysis

Seven loci segregated normally in the CP2 monoploid family (Table 1). Pairwise linkage analysis revealed no linkages among these loci. Four (15 + 16, *STM1004* on linkage group VII; 17 + 18, *STM1049* on linkage group I, 19 + 20, *STM1100* on linkage group VI; and 69 + 70, *STM1017* on linkage group IX) of these eight loci have been mapped to different linkage groups by Milbourne et al. (1998), whereas the locus amplified by primer pair 3 + 4 (*STGBSS* gene) was previously mapped on linkage group VIII by Gebhardt et al. (1991).

The segregation data of the 70 individuals used for gene–centromere mapping are presented in Table 2. A represents the *chc* allele and B represents the *phu* allele at each locus. The codominant nature of SSR markers enables unambiguous detection of both homozygous outcomes (AA and BB); thus the sum of frequencies of homozygous individuals was used to calculate gene–centromere distances that yielded better estimates compared with twice the frequency of nulliplex (*aaaa* · *Aa*; Douches and Quiros 1987). Lack of homozygous genotypes for the *STACCA33* locus amplified by primer pair 15 + 16 verified the FDR nature of CP2 and placed this locus close to a centromere. A heterozygous marker closely linked to the centromere is expected to generate only heterozygous *2n* gametes if the meiotic mechanism of *2n* gamete formation is FDR or its genetic equivalent (Douches and Maas 1998).

Two loci (amplified by primer s3 + 4 and 5 + 6) that showed distorted segregation in the CP2 monoploids segregated normally in the partially heterozygous anther-derived diploids. The segregation data of anther-derived diploids were also used to check for possible linkage between these SSR-containing genes using the SAS procedure FREQ (SAS 1985). No pairs among the eight loci were linked. Two loci (11 + 12 and 23 + 24) were skewed in both the CP2 monoploids and the partially heterozygous anther-derived diploids, therefore the results of the linkage analysis for these loci should be taken cautiously.

### Discussion

Segregation distortion in anther-derived populations has been attributed to the selection of alleles that influence regeneration during the anther culture process or to the expres-

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**Table 2.** Allelic segregation among 70 anther-derived diploids, and gene–centromere mapping for eight SSR loci that were heterozygous in the anther donor (CP2).

<table>
<thead>
<tr>
<th>Primer pair</th>
<th>Locus</th>
<th>Allelic segregation</th>
<th>Map position</th>
<th>95% confidence limits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>AA (freq)</td>
<td>AB (freq)</td>
<td>BB (freq)</td>
</tr>
<tr>
<td>3+4</td>
<td><em>STGBSS</em></td>
<td>19 (0.28)</td>
<td>41 (0.59)</td>
<td>9 (0.13)</td>
</tr>
<tr>
<td>5+6</td>
<td><em>STPROINI</em></td>
<td>13 (0.19)</td>
<td>50 (0.72)</td>
<td>6 (0.09)</td>
</tr>
<tr>
<td>11+12</td>
<td><em>STSTP</em></td>
<td>24 (0.34)</td>
<td>46 (0.66)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>15+16</td>
<td><em>STACCA33</em></td>
<td>0 (0)</td>
<td>68 (100)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>17+18</td>
<td><em>STWIN12G</em></td>
<td>9 (0.14)</td>
<td>50 (0.75)</td>
<td>7 (0.11)</td>
</tr>
<tr>
<td>19+20</td>
<td><em>POTM1-2</em></td>
<td>23 (0.34)</td>
<td>39 (0.57)</td>
<td>6 (0.09)</td>
</tr>
<tr>
<td>21+22</td>
<td><em>ST13ST def 4</em></td>
<td>23 (0.33)</td>
<td>39 (0.57)</td>
<td>7 (0.10)</td>
</tr>
<tr>
<td>23+24</td>
<td><em>STLSI</em></td>
<td>10 (0.14)</td>
<td>34 (0.50)</td>
<td>25 (0.36)</td>
</tr>
</tbody>
</table>

†Deviation from the 1:1 expected ratio. NS, not significant; * significant at 0.05% level; **significant at 0.01% level.

**Fig. 2.** Distorted segregation of the *STSTP* locus, amplified by primer pair 11 + 12, favoring the *chc* 80-1 allele in the backcross population. Lanes from left to right: (1) 100-bp λ DNA ladder; (2) negative control with no DNA; (3) *chc* 80-1; (4) CP2; (5–30) 26 backcross progenies.
sion of lethal or seriously deleterious alleles in a hemizygous condition (Murigneux et al. 1993a, 1993b; Rivard et al. 1996). If the former were the case, then we would expect both of our monoploid populations to exhibit similar allelic preference provided that the anther donors exhibit similar polymorphism. Sexually derived populations should exhibit normal segregation because alleles favored by anther culture would not be expected to have any particular advantage in sexual hybrids. Of the four distorted loci that could be compared in the two monoploid populations, two (amplified by primers 11 + 12 and 21 + 22) exhibited similar distortion, with most monoploids carrying the allele with fewer repeats. However, for the locus amplified by primers 11 + 12, allele B was completely absent in both anther-derived monoploid populations, absent in the anther-derived partially heterozygous diploid population, and under-represented in the CP2 × chc 80-1 backcross. This would indicate lethality rather than selection during anther culture. For the locus amplified by primers 21 + 22, allele A was over-represented in both anther-derived populations but the ratio was only significantly distorted in the BARD 1-3 monoploids. A larger CP2 monoploid population may have revealed similar distortion, making this locus a candidate for allelic selection during anther culture.

Two loci (amplified by primers 3 + 4 and 5 + 6) that exhibited significant distortion in the CP2 monoploid family segregated normally in the BARD 1-3 monoploid family. Therefore, it is unlikely that these loci are linked to genes affecting anther-culture response. Normal segregation was also observed for the locus amplified by primers 3 + 4 in both backcross families. Perhaps the interspecific nature of the CP2 hybrid affected segregation. Specific allelic combinations in CP2 might be responsible for the distortion observed in this locus. The CP2 anther donor was one of only a few vigorous plants that occurred among hundreds of hybrids between accessions of S. chacoense and S. phureja (Veilleux and Miller 1998). All of these interspecific chc × phu hybrids showed severe hybrid breakdown in the form of weak, slow-growing plants with general vigor inferior to either parent. Because of the heterozygous nature of the parental species, either parent might have brought a number of lethal and semi-lethal alleles that in hemizygous condition could compromise the segregation pattern.

The reverse segregation distortion observed in the sexual population (Table 1) for the locus amplified by primer pair 23 + 24 (STLS1) was unexpected. However, genes favoring anther culture response are not necessarily favored in sexual populations.

Unreduced gametes have been used successfully to map genes with respect to the centromere (Douche and Quiros 1987; Bastiaanssen et al. 1996). In these studies, 4x × 2x crosses were used and, depending on the system used (isozymes or morphologic markers), detection of the duplex and nulliplex progenies was not always clear. In our study, the detection of crossover events (that result in duplex or nulliplex progenies in the 4x × 2x crosses), was much easier for two reasons: (i) we used heterozygous anther-derived plants that represented the gametes directly, and (ii) SSRs as codominant markers provided a much better detection of heterozygous vs. homozygous classes. By achieving a clear distinction of both homozygous classes (AA and BB) the sum of their frequencies was used in calculations, thus providing a more precise position of the gene compared with twice the frequency of nulliplex (aaaa) progenies as in the case of most 4x × 2x crosses (aaaa × Aa; Douches and Quiros 1987). Our result in mapping the STGBSS gene on linkage group VIII at a distance of 40.6 cM from the centromere (primer pair 3 + 4) corresponded to that calculated by Bastiaanssen et al. (1996). We are confident that the distances calculated for primer pairs 3 + 4, 5 + 6, 15 + 16, and 17 + 18 were precise and reliable. Distances calculated for the other loci were derived from distorted data. Loci amplified by primer pairs 11 + 12, 19 + 20, and 21 + 22 were skewed in favor of the chc allele and 23 + 24 was skewed in favor of the phu allele. Segregation distortion owing to selection in anther culture or exposure of lethal alleles would severely compromise the data used in HTA, and the calculated distances would be only approximate. That the majority of the SSR loci mapped more than 33 cM from their centromeres supports the hypothesis of a single chromosome per chromosome arm in potato microspores (Bastiaanssen, et al. 1996).

One advantage of monoploid populations for SSR analysis is their lack of heterozygosity. Some SSR analyses have been plagued by the presence of stutter bands that result from heteroduplex formation (Miller and Yuan 1997). As shown in Fig. 1, the monoploids segregate cleanly in agarose gels without stutter bands. By contrast, the heterozygous diploid anther donors in lanes 3 and 4 of Fig. 1 each exhibit three bands instead of the expected two. Because the heaviest band does not occur in the monoploids, it is obviously the spurious one and only the two lighter bands are real. Relative band intensities are insufficient to make this distinction.

Segregation distortion of molecular markers has been observed in androgenic populations of many crops (Foisset and Delourme 1996) with frequencies of distorted loci ranging from 10 (RFLPs; Heun et al. 1991) to 44% (RAPDs and RFLPs; Manninen 2000) within studies of barley. Rivard et al. (1996) found 46 and 70% distorted loci in two anther-derived populations of the weedy potato relative S. chacoense. The absence of lethal alleles in self-pollinated crops removes one origin of distorted segregation. Therefore, more distorted loci can be expected in cross-pollinated crops unless they have been constructed from highly inbred parents. Our results with diploid, primitive potato compare favorably with those of Rivard et al. (1996). As expected, the frequency of distorted SSR markers is towards the high end of the range and may make discovery of genes associated with androgenesis more difficult by confounding with deleterious alleles.

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