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Quantitative trait locus analysis of tuber dormancy in diploid potato (*Solanum spp.*)

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Abstract Quantitative trait locus (QTL) analysis for tuber dormancy was performed in a diploid potato population (TRP133) consisting of 110 individuals. The female parent was a hybrid between haploid *S. tuberosum* (2x) and *S. chacoense*, while the male parent was a *S. phureja* clone. The population was characterized for ten isozyme loci, 44 restriction fragment length polymorphisms (RFLPs) and 63 random amplified polymorphic DNAs (RAPDs). Eighty-seven of these loci segregating from the female parent were utilized to develop a linkage map that comprised 10 of the 12 chromosomes in the genome. Dormancy, as measured by days-to-sprouting after harvest, ranged from 10 to 90 days, with a mean of 19 days. QTLs were mapped by conducting one-way analyses of variance for each marker locus by dormancy combination. Twenty-two markers had a significant association with dormancy, identifying six putative QTLs localized on each of chromosomes 2, 3, 4, 5, 7 and 8. The QTL with the strongest effect on dormancy was detected on chromosome 7. A multilocus model was developed using the locus with highest R^2 value in each QTL. This model explained 57.5% of the phenotypic variation for dormancy. Seven percent of possible epistatic interactions among significant markers were significant when tested through two-way analyses of variance. When these were included in the main-effects model, it explained 72.1% of the phenotypic variation for dormancy. QTL analysis in potato, the methodology to transfer traits and interactions into the 4x level, and QTLs of value for marker-assisted selection, are discussed.

Key words QTLs · Mapping · Isozymes · RFLPs · RAPDs

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Introduction

Tuber dormancy is defined as the obligate period of non-sprouting after harvest even under conditions favorable for sprouting (Simmonds 1964). Dormancy release, as reviewed by Hemberg (1985), involves changes in respiration and levels of enzymes, sucrose, nitrogenous compounds and endogenous hormones in the tuber. Current literature supports an "inhibitor/promoter" hypothesis, with critical events associated with dormancy release involving a shift in the growth regulator ratio in favor of promoters, and subsequent establishment of positive feedback between the bud and mobilized food reserves (Coleman 1987).

The length of dormancy varies among different potato varieties (Burton 1963; Simmonds 1964; Bogucki and Nelson 1980; Jeoung et al. 1983). This is an important trait in potato production, since long-term storage without sprout growth is critical for tuber marketing. One method used to prolong tuber dormancy is low-temperature storage (4°C). However, this causes a conversion of non-reducing to reducing sugars, which is undesirable for the processing industry. Various dormancy-inducing chemicals have also been tried (Burton 1966) but questions concerning their toxicologies were raised (Vaughn and Spencer 1991), and some have been banned from use. An alternative approach is to increase the length of dormancy through genetic means. Long dormancy has been identified in selections made from South American diploid tuber-bearing relatives of the potato (Thompson et al. 1980; Hermundstad and Peloquin 1985; Hermundstad 1986) and this characteristic can be introgressed into the cultivated gene pool.

Tuber dormancy is under polygenic control (Simmonds 1964), and more than three genes are involved (Flewelling 1987). Quantitative trait locus (QTL) analysis using molecular markers (Lander and Botstein 1989) provides a tool for a more detailed study of this trait. The numbers and genomic distribution of quantitative trait loci and their contribution to trait variation can be estimated. This knowledge is necessary to be able to monitor the introgression

of these genes and provide a framework for a more analytical breeding of the potato using wild relatives. Isozymes and RFLPs have been used for dissecting quantitative traits in maize (Edwards et al. 1987; Stuber et al. 1987), tomato (Tanksley et al. 1982; Paterson et al. 1988; Tanksley and Hewitt 1988; Weller et al. 1988), soybean (Keim et al. 1990; Diers et al. 1992), wheat (Miura et al. 1992), and barley (Hackett et al. 1992; Hayes et al. 1992; Heun 1992). In a previous study we reported on the use of isozymes to identify QTLs for specific gravity and dormancy in potato (Freyre and Douches 1994). In the present study, QTL analysis of tuber dormancy has been complemented through the use of previously-mapped RFLPs and unmapped RAPD markers.

Materials and methods

Plant material

One of the two populations previously utilized by Freyre and Douches (1994) was chosen for this study. This population, named TRP133, is diploid and consists of 110 F_1 genotypes. The female parent used in the cross was clone 84SD22, a hybrid between haploid *S. tuberosum* (2x) and *S. chacoense*, while the male parent was *S. phureja* clone 84S10. The parents were chosen because of long and very short dormancy periods, respectively, and previously-known isozyme diversity. The initial population consisted of 220 progeny. Seedlings were transplanted to the field at Montcalm Research Farm, Edmore, Michigan, in 1989. Due to the lateness of the material, many genotypes had not tuberized after 4 months and were discarded for future studies.

Measurement of dormancy

Four tubers of 3–5 cm diameter per genotype were selected after harvest from 1989 seedling field plots. These were placed on trays and stored at 10°C in the dark, which are common storage conditions, and then evaluated weekly. Length of dormancy was determined as the average number of days required for 2-mm-long sprouts to be evident for each genotype.

Genotyping

The parents were characterized for the morphological marker yellow flesh (Y), as well as for isozymes, RFLPs, and RAPDs.

(1) Isozyme analysis: ten segregating isozyme loci (*Dia-1, Est-1, Got-1, Got-2, Idh-1, 6-Pgdh-3, Pgi-1, Pgm-1 Pgm-2, Prx-3*) were utilized as described in Freyre and Douches (1994).
(2) RFLP analysis: the tomato genomic and cDNA probes utilized were provided by S. Tanksley, Cornell University, and potato genomic and cDNA probes by C. Gebhardt, Max Planck Institut, Germany. At least four markers per chromosome were selected based on their position on previous potato maps (Bonierbale et al. 1988; Gebhardt et al. 1991; Tanksley et al. 1992). DNA was extracted from leaf tissue for all genotypes following the procedure of Saghai-Maroof et al. (1984). The concentration was quantified using a fluorometer (Hoefer Scientific Instruments, Model TKO 100). Seven micrograms of DNA were digested with the following endonucleases using two units of enzyme per µg of DNA: *Eco*RI, *Hin*dIII, *Xba*I, *Dra*I, *Eco*RV, *Bam*HI. Digested DNA samples were separated on 0.8% agarose gels. Southern transfer onto Nytran nylon membranes (Schleicher and Schuell), oligolabelling of probes with ^{32}P, filter hybridization and washes were all performed according to Sisco et al. (1990). Filter hybridization was done using a Robbins Scientific Incubator (Model 310). Filters were enclosed in plastic wrap and placed in X-ray cassettes at –80°C for 2–10 days.

(3) RAPD analysis: the PCR protocol followed Williams et al. (1990) with minor modifications to optimize for potato DNA. Each reaction was composed of: 1×buffer (100 mM KCl, 100 mM Tris-HCl pH 8.3), 0.8 mM dNTPs, 5 mM $MgCl_2$, 1 U Stoeffel enzyme (Perkin Elmer Cetus), 12.5 ng of primer and 12.5 ng of potato DNA brought up to a final volume of 12.5 µl with ddH_2O. The thermocycler (Perkin Elmer Cetus DNA Thermocycler 480) was programmed for three cycles of 1 min at 94°C, 1 min at 35°C, and 2 min at 72°C; followed by 34 cycles of 1 min at 94°C, 1 min at 40°C, and 2 min at 72°C; and 5 min extension at 72°C. On completion, amplification products were separated by electrophoresis on a 1.6% agarose gel in 1×TAE buffer. Lambda DNA cut with *Eco*RI and *Hin*dIII was used as the fragment size marker.

The primers employed were commercial 10-mers from Operon Technologies (Alameda, California), specifically from Kits A, F, G, H and I. Primers were selected when they generated bands in one parent and not in the other. Because of complete dominance in these markers, the heterozygous and homozygous forms for the presence of an allele in a parent could not be distinguished until the band was observed either to segregate or to be present in all the progeny, respectively. The nomenclature of amplified fragments followed Quiros et al. (1993).

Construction of linkage map

Markers which were in heterozygous form in the female parent 84SD22 were utilized to develop the linkage map. The LINKAGE-1 program (Suiter et al. 1983) was used to determine the fit to expected Mendelian ratios for each marker. The map was then constructed with MAPMAKER (Lander et al. 1987) v.01 for Macintosh, using LOD scores exceeding 3.0. Linkage groups were assigned to specific chromosomes based on previously-mapped isozyme and RFLP loci (Bonierbale et al. 1988; Tanksley et al. 1992); RAPD markers were subsequently added.

Statistical analyses

Statistical analyses were performed for markers that were heterozygous in one parent and homozygous in the other, where a BC_1-type segregation (1:1) was expected. The methods used have been previously described in Freyre and Douches (1994). Briefly, for each of these markers the population was divided into two groups based on the segregation of the marker. Single-factor ANOVAs between dormancy data and each marker locus were conducted (PROC GLM, Statistical Analysis Systems, Cary, NC). Markers with distorted segregation ratios were not used in the analyses. F tests were used to test if the means of genotypic marker classes were statistically different ($P< 0.05$). A significant difference in dormancy means was interpreted as linkage of a QTL to the marker locus. For linked markers, the phenotypic effect of the marker allele was estimated by the difference between the dormancy means of the two genotypic classes. QTLs were localized based on the position of marker loci on the map. Significant markers in the same chromosome were considered as one QTL if the distance between them did not exceed 50 cM (Paterson et al. 1991). Loci with the highest R^2 value per QTL were then combined in a multiple analysis of variance model to predict the total variation for dormancy explained by the identified QTLs (Keim et al. 1990).

Epistatic interactions between significant loci were tested by two-way analyses of variance. Significant interactions were then included in the multiple analysis of variance to determine their contribution to the phenotypic variation for dormancy. When there were several interactions between the same pairs of QTLs, the one with the highest R^2 value was utilized. If not already present, the main effect of the loci in the interactions were also included in the model.

Results

The average number of days-to-sprouting was 80 and 10 days for the female and male parents, respectively. The distribution of values in the population was continuous but highly skewed towards short dormancy, having a range from 10 to 90 days and a mean of 19. Therefore, a $\log_{10}$ transformation of the number of days-to-sprouting was used to improve normality. The frequency distribution of these values is shown in Fig. 1. Two progeny (designated as TRP133-1 and TRP133-215) had dormancy periods of 90 and 87 days, respectively, which was longer than the female parent dormancy period. The dormancy length for TRP133-1 was significantly different than that of the female parent.

All isozyme loci fit the expected segregation ratio, as previously described (Freyre and Douches 1993). For all RFLP probes evaluated in the parents, only one (TG83) was found to be heterozygous for the same alleles in both parents thus having an F_2-type (1:2:1) segregation. Data from this probe were not included in the analysis. All other probes resolved loci heterozygous in one of the parents, and homozygous in the other. Thirty-four RFLP probes that segregated in a BC_1 (1:1) fashion were scored. Eight of these resolved two loci and were designated by the addition of T or B (for top and bottom locus), respectively. Additionally, loci TG122T and TG152T showed triallelic segregations: both parents had one unique allele with the other in common, resulting in four genotypic classes in the progeny. In these cases the presence of the unique allele from each parent was scored independently. The total number of RFLP loci that were scored was 44. The expected segregation ratio was found for all loci except TG141, TG18, TG53 and CD31. The female and male parents were heterozygous for 32 and 12 loci, respectively. With respect to RAPDs, a total of 29 random primers were utilized in this study. These produced a range of 1–5 scorable loci, resulting in a total of 63 RAPDs scored in the progeny. Eight of the RAPDs had distorted segregation ratios (data not shown). The female and male parents were heterozygous for 50 and 13 loci, respectively.

The linkage map developed with isozyme, RFLP and RAPD loci which were in heterozygous form in the female parent is shown in Fig. 2. None of the RFLP probes selected by their known location on chromosomes 9 and 12 showed polymorphism or could be scored successfully, so no markers could be assigned to these chromosomes. The RAPD markers included in the map, and the size of the amplified fragments, is shown in Table 1. The size of these fragments ranged between 0.5 and 1.4 kb. Some of the RAPD loci scored could not be mapped, either because they showed linkage only to other RAPD loci, or no linkage to any other locus.

One-way ANOVAs were conducted between tuber-dormancy data and the two genotypic classes for each of the markers used. In addition to a significant association with six previously-described isozyme loci (Freyre and Douches 1994), significant QTLs were found with one RFLP locus and 15 RAPDs (Table 2). Genotype TRP133-1 with a dormant period of 90 days and TRP-215 with 87 days, had 82% and 95% of the alleles linked to long dormancy for the 22 significant markers, respectively. The significant RFLP locus (TG31B) and four of the significant RAPD loci were heterozygous in the male parent. These loci showed no linkage between each other and their chromosomal location has not been established. The position of the significant loci segregating from the female parent is shown in Fig. 2. These markers identify six QTLs, one on each of chromosomes 2, 3, 4, 5, 7 and 8.

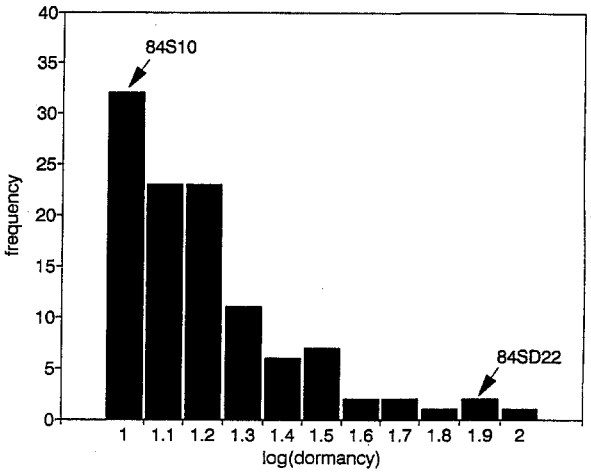

Fig. 1 Frequency distribution of dormancy period ($\log_{10}$ transformed) in diploid potato population TRP133. 84SD22 and 84S10 are the female and male parents, respectively

The amount of phenotypic variation for tuber dormancy explained by each significant marker, as determined by its R^2 value, ranged from 4.2% to 20.4%. This represents a difference of 3.6 and 7.7 days-to-sprouting between genotypic class means for the markers, respectively (Table 2). Most frequent R^2 values were between 4% and 6% (36% of all markers) and between 14% to 16% (22%). On average, loci on the QTL of chromosome 7 had the highest R^2 values, all of them being above 12%. This represented a difference of more than 5 days-to-sprouting between means of the genotypic classes. The isozyme marker *Got-2* on this same QTL had markedly the highest effect of all loci, explaining 20.4% of the phenotypic variation.

Seventeen out of two-hundred-and-thirty-one possible epistatic interactions (7%) were significant (Table 3). Most of these interactions involve one marker that was heterozygous in the male parent with others heterozygous in the female parent, so that the two chromosomal locations involved could not be identified. In the cases where the interaction was between two loci segregating from the female parent, it involved loci on chromosomes 3 and 7 (G19.1**Got-2*), and 5 and 7 (G05.1 with others). The phenotypic variation of dormancy explained by each of these interactions ranged between 3.5% and 7.1%, and more than half of them (53%) explained between 4% and 6% of the variation.

The marker with the highest R^2 value per QTL was chosen to develop a multilocus model. All significant mark-

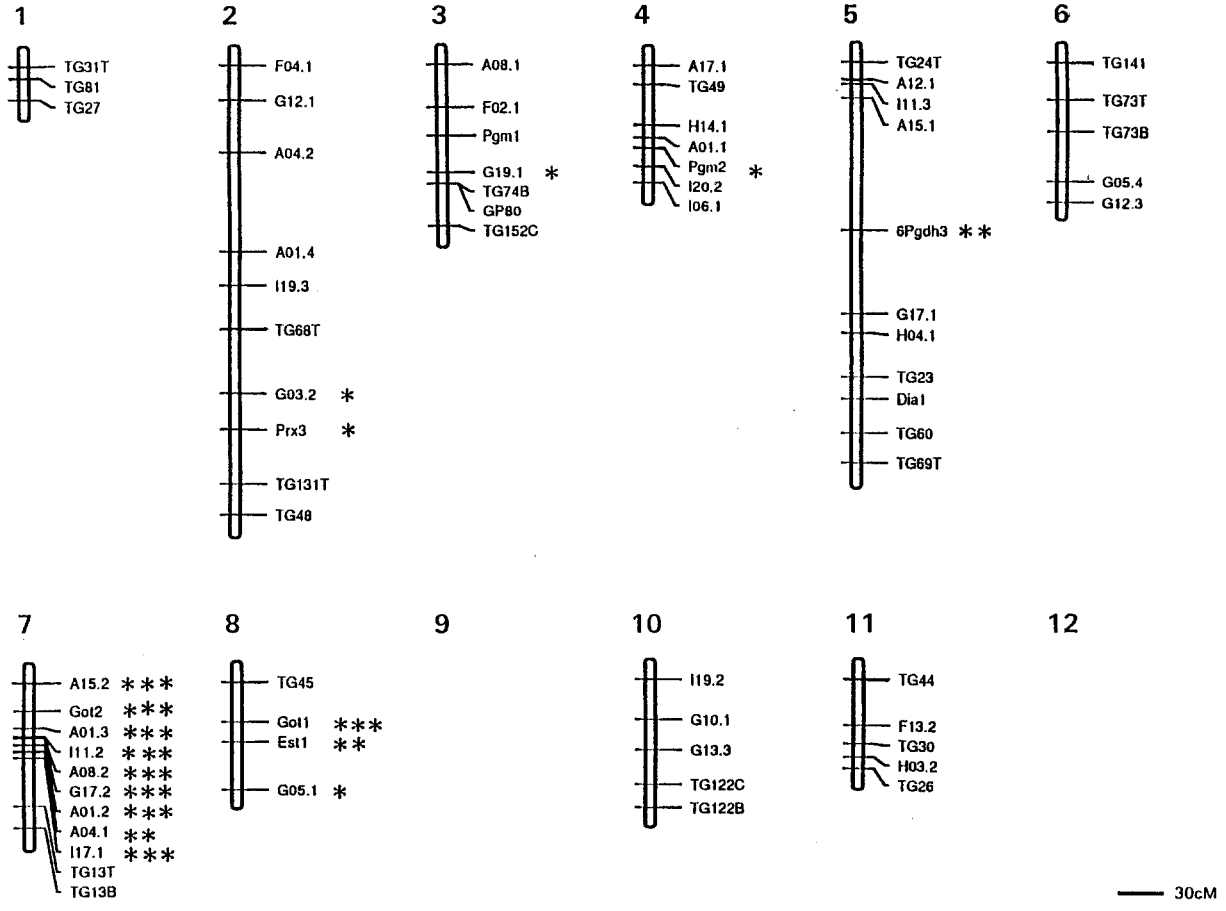

Fig. 2 Molecular linkage map and localization of QTLs for tuber dormancy in the diploid potato population TRP133. Significant markers are indicated by *asterisks* on the right side of their name. *, **, *** indicate 0.05, 0.01 and 0.001 probability levels, respectively

Table 1 RAPD markers included in the QTL analysis for tuber dormancy in diploid potato

RAPD[a]	Size (kb)	RAPD	Size (kb)
A01.1	0.6	G05.4	1.2
A01.2	0.8	G10.1	1.0
A01.3	1.2	G12.2	1.2
A01.4	1.4	G12.3	1.4
A04.1	0.9	G13.1	0.5
A04.2	1.1	G13.3	0.9
A08.1	1.4	G17.1	0.6
A08.2	1.4	G17.2	0.9
A12.1	1.2	G19.1	0.58
A15.1	0.6	H03.2	0.9
A15.2	0.8	H04.1	0.98
A17.1	1.2	H14.1	0.75
F01.2	1.3	I06.1	0.9
F02.1	0.6	I11.2	0.95
F04.1	0.7	I11.3	1.2
F05.1	1.4	I17.1	0.6
F13.2	1.3	I19.2	0.83
G03.2	0.9	I19.3	1.1
G05.1	0.5	I20.2	0.83

[a] Nomenclature of RAPDs obtained with Operon 10-mer primers follows Quiros et al. 1993

ers heterozygous in the male parent were also included. Accordingly, a model with the markers *Pgm-2*, *6-Pgdh-3*, *Got-2*, *Got-1*, *F01.2*, *F05.1*, *G03.2*, *G12.2*, *G13.1*, *G19.1* and TG31B was developed, which explained 57.5% of the phenotypic variation for dormancy. This value increased to 72.1% when the significant interactions were included (Table 4).

Discussion

The distribution of number of days-to-sprouting for population TRP133 was highly skewed towards short dormancy, which may be explained by dominant genes coming from the *S. phureja* male parent. Although a normal distribution of values is preferred for QTL analysis, studies have been previously performed in tomato for traits with skewed distributions (Nienhuis et al. 1987; Paterson et al. 1991). Some degree of transgressive segregation was also observed in the population, since two genotypes have even longer dormancy periods than the female parent.

In previous cases of mapping with heterozygous parents in potato, loci segregating from both parents were combined in one map by linkage to markers for which both of them were heterozygous (Bonierbale et al. 1988), with the formation of what has been designated as "allelic bridges" (Ritter et al. 1990). In the present case, all iso-

Table 2 Significant association between markers and tuber dormancy in diploid potato

Loci[a]	Chromosome location.[b]	R^2 (%)	Phenotypic effect (days)[c]
Heterozygous in ♀:			
Prx-3	2	5.2*	3.8
G03.2	2	5.4*	4.3
G19.1	3	4.3*	3.4
Pgm-2	4	5.5*	3.8
6-Pgdh-3	5	6.9**	4.2
A15.2	7	14.4***	6.3
Got-2	7	20.4***	7.7
A01.3	7	14.6***	6.5
I11.2	7	15.5***	6.9
A08.2	7	13.4***	5.9
G17.2	7	15.7***	6.7
A01.2	7	15.0***	6.4
A04.1	7	12.4**	5.8
I17.1	7	13.7***	6.1
Got-1	8	9.0***	5.0
Est-1	8	5.8**	4.0
G05.1	8	4.2*	3.6
Heterozygous in ♂:			
F01.2	–	10.5**	5.7
F05.1	–	8.4**	4.8
G12.2	–	5.2*	3.7
G13.1	–	4.6*	3.5
TG31B	–	7.2**	4.6

[a] Isozyme loci are italicized. TG31B is a RFLP locus; others are RAPD markers
[b] Chromosomal location for markers heterozygous in the male parent have not been identified
[c] Indicates the phenotypic difference between the trait means of the markers classes, in days-to-sprouting
*, **, *** indicate significance at the 0.05, 0.01 and 0.001 probability levels, respectively

Table 3 Significant epistatic interactions between significant markers for tuber dormancy in diploid potato

Interaction	R^2 (%)
Heterozygous in ♀:	
G03.2* *Prx-3*	4.9*
G05.1* G17.2	3.9*
G05.1* I11.2	5.5*
G05.1* I17.1	3.8*
G05.1 * A01.3	6.4**
G05.1 * A01.2	4.0*
G05.1 * A04.1	3.5*
G05.1 * A08.2	3.6*
G19.1 * *Got-2*	4.2*
Heterozygous in ♂ [a]:	
F01.2 * F05.1	4.6 *
F01.2 * G12.2	5.4 *
F01.2 * TG31B	7.1 **
F05.1 * TG31B	6.2 *
F05.1 * *Prx-3*	5.7 *
G12.2 * G19.1	5.5 *
G12.2 * *6-Pgdh-3*	5.5 *
TG31B * *Prx-3*	6.4 **

[a] One or both of the loci in the interaction are heterozygous in the male parent
*, ** Indicate significance at the 0.05 and 0.01 probability levels, respectively

Table 4 Loci chosen for multilocus models used to determine the amount of phenotypic variation for tuber dormancy explained by QTLs and epistatic interactions

Loci	R^2 (%)
Main-effects model:	
Pgm-2	57.5 ***
6-Pgdh-3	
Got-2	
Got-1	
G03.2	
G19.1	
F01.2	
F05.1	
G12.2	
G13.1	
TG31B	
Interactions:	
Prx-3	72.1 ***
Pgm-2	
6-Pgdh-3	
Got-2	
Got-1	
G03.2	
G19.1	
G05.1	
A01.3	
F01.2	
F05.1	
G12.2	
G13.1	
TG31B	
F01.2* F05.1	
F01.2* G12.2	
F01.2* TG31B	
F05.1* TG31B	
F05.1* *Prx-3*	
G03.2* *Prx-3*	
G05.1* A01.3	
G12.2* G19.1	
G12.2* *6-Pgdh-3*	
G19.1* *Got-2*	
TG31B* *Prx-3*	

*** Indicates significance at the 0.001 probability level

zyme and RFLP markers were heterozygous in either one of the parents, with the exception of only one RFLP locus, which was heterozygous in both. Most markers were heterozygous in the female parent, which is an interspecific hybrid between *S. tuberosum* and *S. chacoense*. Therefore, a linkage map with the markers segregating from this parent was constructed. The linear order of isozyme and RFLP markers is the same as in previous potato maps (Bonierbale et al. 1988; Tanksley et al. 1992), although recombination distances differ. This may be due to the utilization of different species in the mapping population.

In the map developed in the present study, we incorporated a total of 35 RAPDs. We find that these markers show high polymorphism and repeatable results in potato. While the number of isozyme loci is limited, there is an immense number of random primers available for use, many of which resolve several segregating loci. The PCR technique is relatively simple, and the time necessary to obtain re-

sults is short as compared with RFLP analysis. These characteristics make RAPD markers a valuable addition to QTL analysis and marker-assisted techniques, particularly in backcross populations which have only two genotypic classes.

A significant association was found between tuber dormancy and 22 markers. Seventeen of these markers were heterozygous in the female parent and identified six QTLs, one on each of chromosomes 2, 3, 4, 5, 7 and 8. Additionally, five markers segregating from the male parent also showed significant association with dormancy. These loci were not linked to each other, and their chromosomal location could not be established. The two individuals with the longest dormant periods in the population had 82% and 95% of alleles linked to long dormancy for the significant marker loci.

On each of chromosomes 3, 4 and 5, only one significant marker was identified. On chromosome 5, this may be due to the fact that *6-Pgdh-3* is not closely linked to any other marker. For *Pgm-2* on chromosome 4, the effect of this QTL might be too small to be detected with other linked markers, while G19.1 on chromosome 3 has a high *P* value (P=0.049) and might be a false positive. The highest number of significant markers was identified on chromosome 7. On this chromosome nine markers, eight of which are RAPDs, are clustered on a region spanning 49 cM.

The values of R^2 for individual markers ranged between 4.2% and 20.4% which represents a difference of 3.3 and 7.7 days-to-sprouting between means of the genotypic classes for the markers, respectively. On average, the highest effect on dormancy is by markers on chromosome 7, each of which contributes more than 12% of the phenotypic variation of dormancy. The isozyme marker *Got-2* has markedly the highest effect, explaining 20.4% of the variation. All significant loci on this QTL were segregating from the female parent. This QTL thus constitutes an important region of the genome associated with long dormancy and would be a strong candidate for marker-assisted introgression.

A total of 7% of the possible epistatic interactions between significant markers were also significant in this study, as compared with 3% and 1% in two different studies in maize (Edwards et al. 1987; Stuber et al. 1992). When these were included in the multiple-analysis model, the amount of phenotypic variation of dormancy explained by the markers was 72.1%, giving an increase of 25.4% (14.6/57.5) over the main-effects model. Therefore, epistatic interactions seem to be contributing significantly to dormancy variation. To maintain these interactions in future generations, transfer of intact portions of the genome might be necessary. In potato breeding, improved 2x germplasm is transferred to the cultivated 4x level using 2n gametes (Chase 1968; Iwanaga 1983; Peloquin et al. 1989). These gametes are produced either by genetically equivalent FDR (first division restitution) or SDR (second division restitution) mechanisms. 4x-2x crosses with FDR gametes might be more appropriate in breeding for this trait since they transfer approximately 80% of the genome intact from parent to offspring, thus maintaining a large fraction of epistatic interactions (Peloquin and Ortiz 1991).

This study in potato differs from traditional QTL studies performed on inbreeding crops. The generation of inbred parents in potato is not practicable due to self-incompatibility and inbreeding depression at the 2x level. Therefore, heterozygous parents must be used to develop the mapping population, and both parents can contribute markers associated with the trait. Secondly, utilization of 0.01 or 0.001 significance levels have been suggested to avoid identification of false positives (Lander and Botstein 1989). In this first QTL study on dormancy, we decided to use the less stringent level of 0.05 as indicated by Soller and Brody (1976). We have also incorporated RAPD markers in the QTL analysis, which has not been previously reported. The markers we utilized are not evenly spaced in the map and information for two chromosomes is missing. Although we recognize that we did not completely survey the potato genome, we identified six putative QTLs which explain 57.5% of the phenotypic variation for tuber dormancy. Furthermore, the QTL identified on chromosome 7, which has a significant effect upon tuber dormancy, may indicate major gene control of this complex trait, and could be used in marker-assisted selection.

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