Theor Appl Genet (2005) 110: 1068–1073
DOI 10.1007/s00122-005-1927-6

ORIGINAL PAPER

Xiu-Qing Li · Hielke De Jong · Darlene M. De Jong
Walter S. De Jong

Inheritance and genetic mapping of tuber eye depth in cultivated diploid potatoes

Received: 31 October 2004 / Accepted: 6 January 2005 / Published online: 18 February 2005

Abstract Tuber eye depth of the potato (*Solanum tuberosum* L.) is an important trait for the processing quality and appearance of potatoes. In the present study, we used a cultivated diploid potato family (12601) of 107 plants to dissect the mode of inheritance and to map the gene(s) controlling the trait. The family segregated for both eye depth (deep vs shallow) and tuber shape (round vs long) traits. The deep eye (*Eyd*) phenotype was found to be associated with round tubers (*Ro*) in most progeny clones. Further evaluation of this population with molecular markers including simple sequence repeats, amplified fragment length polymorphism, and sequence-characterized amplified regions revealed that the primary locus for eye depth is located on chromosome 10. This map location was confirmed by evaluating a second diploid family (12586). The results of this study led to the following conclusions: (1) there is a major locus controlling the eye depth trait; (2) deep eye (*Eyd*) is dominant to shallow (*eyd*); (3) the *Eyd*/*eyd* locus is located on chromosome 10; and (4) the *Eyd*/*eyd* locus is closely linked with the major locus for tuber shape (*Ro*/*ro*), at a distance of about 4 cM.

Keywords Tuber morphology

Communicated by C. Möllers

X.-Q. Li (✉) · H. De Jong
Research Scientist of Molecular Genetics,
Potato Research Center, Agriculture
and Agri-Food Canada, P.O. Box 20280,
850 Lincoln Rd., Fredericton, NB, Canada, E3B 4Z7
E-mail: lixq@agr.gc.ca
Tel.: +1-506-4524829
Fax: +1-506-4523316

D. M. De Jong · W. S. De Jong
Department of Plant Breeding and Genetics,
Cornell University, Ithaca, NY 14853-1901, USA

Introduction

Eye depth is a major component of tuber "quality." Deep eyes detract from the appearance of tubers and add to the cost of peeling in processing factories. This trait has been included in genetic investigations throughout the twentieth century (Table 1). The hypotheses that have been put forward have on some occasions been contradictory. These disagreements may be due to several reasons including:

1. Several early studies were based on very small populations. It is now understood that great care must be taken in the extrapolation from such populations to a hypothesis of inheritance.
2. The previous studies were conducted with tetraploid ($2n = 4x = 48$) potatoes. The results from populations with tetrasomic inheritance can be difficult to interpret. Such difficulties are exacerbated when relatively small populations are used for genetic analysis.
3. Several authors found that the eye depth trait is subject to modification by environmental factors.

The cultivated diploids ($2n = 2x = 24$) provide excellent opportunities for the study of many genetic traits, including tuber eye depth. In segregating populations, the disomic inheritance pattern of the diploids allows for much simpler ratios than are possible with tetraploids. Over the past several decades, populations of well-adapted, male- and/or female-fertile diploids that produce large tubers under field conditions have been developed at the Potato Research Centre, Agriculture and Agri-Food Canada, in Fredericton, New Brunswick. The materials were originally derived from crossing haploids of *Solanum tuberosum* with primitive cultivated diploids such as *S. phureja* and *S. stenotomum*. These diploid populations have been used for studying the inheritance and genetic mapping of several traits such as tuber flesh color (De Jong 1987), light green foliage mutant (De Jong et al. 1998), and tuber shape (De Jong and Burns 1993). Some of these well-adapted

Table 1 Hypotheses on the inheritance of eye depth in chronological order

Reference	Hypothesis
East (1910)	Shallow eyes are probably dominant over deep
Salaman (1911)	Deep eyes are dominant over shallow. Experiments did not show any relationship between eye depth and tuber shape
Nilsson (1913)	Eye depth is controlled by one gene. Deep eyes are dominant over shallow
Huber (1930)	Deep eyes are dominant over shallow. Shallow eyes are controlled by two complementary genes
Black (1930)	Eye depth is controlled by genetic factors. The extreme types (very deep and very shallow) are probably homozygous, and the intermediate types are heterozygous. Eye depth is greatly affected by environmental conditions
Von Rathlef and Siebeneick (1934)	Eye depth is very strongly influenced by environmental factors. A major gene controls both eye depth and some irregular shapes such as flat and knobby
Feistritzer (1952)	Progeny obtained by selfing has a high proportion of clones with shallow-eyed tubers
Maris (1962, 1966)	Extensive review of previous hypotheses. On basis of own large volume of painstaking research concluded that eye depth is controlled by one major gene, *O*, with a cumulative effect. This gene is linked with a major gene, *K*, controlling tuber shape. Eye depth is very subject to modification by environmental factors

diploid clones have also been observed to consistently produce tubers with deep eyes, while others consistently yield tubers with shallow eyes.

Several genetic maps of potato have been constructed using restriction fragment length polymorphism (RFLP) (Bonierbale et al. 1988; Gebhardt et al. 1991), amplified fragment length polymorphism (AFLP) (van Eck et al. 1994, 1995), and simple sequence repeat (SSR) markers (Milbourne et al. 1998). Mapped RFLP and SSR markers are especially useful in providing anchor markers of known chromosomal location when mapping in new populations, while AFLP technology is well suited towards rapidly generating large numbers of markers to fill out the gaps between anchor loci.

To resolve some of the previously reported disagreements regarding the inheritance of eye depth, this investigation was undertaken using well-adapted, cultivated diploid potatoes. RFLP, SSR, and AFLP markers were also used to genetically map the trait. Since the genes controlling eye depth and tuber shape may be linked (Maris 1966) and the major gene for tuber shape has been mapped to chromosome 10 (van Eck et al. 1995), we prioritized chromosome 10 during genetic mapping.

Materials and methods

Plant materials

Primary phenotyping of eye depth and genetic mapping was conducted using a progeny (family 12601) of 107 clones from two well-adapted diploid parents. The female parent, 11379-03, has long tubers with shallow eyes, and the male parent, 08675-21, has round tubers with deep eyes (Fig. 1). This population was grown and evaluated at the Agriculture and Agri-Food Canada Potato Breeding Substation in Benton Ridge, New Brunswick, Canada.

A second diploid family (12586), generated by crossing 10909-18 (long tuber and shallow eyes) as female with 08675-21 as male, was used to confirm the map location for the major locus of eye depth. Family 12586 was grown in Ithaca, New York, USA, and phenotyped following similar methods as for family 12601. For 12586 only progeny with extreme phenotypes (tubers with unambiguously deep eyes or unambiguously shallow eyes) were used in molecular marker analysis.

Phenotyping of eye depth and tuber shape

The determination of eye depth and tuber shape on the progeny tubers was conducted on field-grown tubers of second and subsequent generations. Both traits were

Fig. 1 Representative tubers of parents 11379-03 and 08675-21

scored in three categories: for shape as long, oval, or round; and for eye depth as shallow, medium, or deep. The scoring was repeated for three years with about 8–50 tubers for each clone each year.

DNA extraction

DNA was extracted from both field-grown tubers and greenhouse plant leaves. Since AFLP technology can generate DNA fragments from both potato DNA and any contaminant DNA, we sterilized the surface of the potato materials used in the analysis to avoid or reduce the problem of potential contamination. Prior to DNA extraction, potato tubers and leaves were surface-sterilized with 70% ethanol for 10 s, rinsed twice with autoclaved water, then re-sterilized in a bleaching solution containing 1% sodium hypochlorite for 2 min, followed by rinsing three times with autoclaved water. Tuber DNA was extracted according to a previously described method (Li et al. 1996). Leaf DNA was isolated with a DNA extraction kit from Invitrogen Canada, Burlington, Ont., Canada (formerly BRL Life Technologies), following the manufacturer's instructions.

Anchor molecular markers, DNA sequencing, and primer design

DNA clones of a selected set of anchor markers including CT125 and CT240 for tomato chromosome 10 were kindly provided by Dr. S. Tanksley, Cornell University. Potato DNA clone CP105 was kindly provided by Dr. C. Gebhardt, Max Planck Institute. The plasmids were sequenced using a Big Dye Terminator Cycle Sequencing Kit from PerkinElmer Biosystems (PerkinElmer, Norwalk, Conn., USA), because either of the unavailability of nucleotide sequences of the RFLP markers at the time or to confirm identity of the plasmids. Polymerase chain reaction (PCR) primers were designed for mapping from the nucleotide sequences of the DNA clones. Primer synthesis was by Operon Technologies (Alameda, Calif., USA).

PCR amplification for mapping molecular markers

DNA amplification was carried out in a total reaction volume of 20 µl containing 1× PCR reaction buffer (50 mM KCl, 10 mM Tris of pH 8.3, and 2 mM $MgCl_2$), 10 ng template DNA, 0.5 U *Taq* DNA polymerase from PerkinElmer Biosystems, 0.4 mM each dNTP (dATP, dCTP, dGTP, and dTTPs), and 0.5 µM of each primer. All the amplifications were conducted using the GeneAmp PCR System 9700 from PerkinElmer Biosystems. The reaction parameters were as follows: (1) 94°C for 5 min; (2) 30 cycles of 1 min at 94°C, 1.5 min at 50°C, and 1.5 min at 72°C; (3) 7 min at 72°C.

Agarose and polyacrylamide gel electrophoresis

The amplified PCR products were resolved in 2% agarose gels containing 1× TBE buffer (89 mM Tris-base, 89 mM boric acid, and 2 mM EDTA, pH 8.3) or in 6–6.5% polyacrylamide gels with 1× TBE, then visualized by staining with 0.5 µg/ml ethidium bromide for agarose gels or by silver staining for polyacrylamide gels. Agarose gels were photographed under ultraviolet light with a Digital Imaging System (GelDoc, Bio-Rad, Hercules, Calif., USA).

AFLP analysis

To generate markers distributed across the whole genome, AFLP analysis was conducted with leaf DNA, using the AFLP kits (AFLP Starter Primer Kit, cat. no. 10483-014; AFLP Core Reagent Kit, cat. no. 10482-016) from Invitrogen Canada, following the manufacturer's instructions. Radioactive labelling was with the isotope ^{33}P, and radiography was conducted with Kodak X-ray film.

Mapping

The scoring of AFLP bands after radiography was with the presence–absence method. Only bands that could be unambiguously scored were used in mapping. SSR products were scored according to the allele combinations if multiple codominant alleles were observed, or with presence–absence scores if only a single strong band was observed or if the codominance was not obvious. The mapping analysis was conducted using JoinMap, version 3.0, with the *complete-population* (CP) option at LOD scores of 4, without using the *fixed-order* function. The map was formatted with MapChart, version 2.1.

The linkage between the major eye depth locus detected in family 12601 and molecular markers was further tested using family 12586. This family originally consisted of 171 individuals, of which 85 were deemed to have deep eyes, while 46 had shallow eyes and 40 had eyes of intermediate depth. Genomic DNA was isolated from leaves of 47 clones with deep eyes and 41 clones with shallow eyes, using a Qiagen miniprep kit. These DNA samples were then evaluated with SSR marker STM1106, as described above.

Results

Genetic segregation

Tuber eye depth (deep vs shallow) segregated in Mendelian fashion in family 12601 and appeared to be associated with tuber shape (Table 2). In this family, 47 clones had deep eyes, 50 clones had shallow eyes, and nine clones had tubers with intermediate eye depth. For

Table 2 Segregation for eye depth and tuber shape in family 12601

Family	Parents		Tuber shape	Eye depth			Total
	Female	Male		Deep	Medium	Shallow	
12601	11379-03	08675-21	Round	45	6	1	52
			Oval	3	2	3	8
			Long	0	1	46	47
			Total	48	9	50	107

the nine intermediate clones, three were more close to the deep type, two were more close to the shallow type, and four could not be assigned to deep or shallow. None of the 48 clones with deep eyes had long tubers. Among the 50 shallow-eyed clones, only one had round tubers. This association suggests linkage between major genes controlling eye depth and tuber shape. We postulate that eye depth is mainly controlled by a single gene for which the gene symbol *eyd* is proposed. The *Eyd* genotypes would have deep eyes, and the *eydeyd* genotypes would have shallow eyes.

Molecular mapping

Primers defining SSR and AFLP markers linked with *Eyd* and *Ro* are presented in Table 3. The CP105, CT125, and CT240 markers listed in Table 3 were all PCR-based markers, where the primers were based on the nucleotide sequence of potato RFLP marker CP105 and tomato RFLP markers CT125 and CT240, respectively.

Eyd and *Ro* were mapped to the same linkage group, 4 cM apart (Fig. 2). Five anchor markers from chromosome 10 (Bonierbale et al. 1988) including CT240 (Tanksley et al. 1992), CP105 (Gebhardt et al. 1991, 1993), and two SSR markers (STM0051 and STM1106) (Milbourne et al. 1998) mapped to the same linkage group as *Eyd* and *Ro*. Therefore, the *Eyd*/*eyd* locus is located on chromosome 10.

Several chromosome 10 markers from the male parent were correlated with eye depth, indicating that the male parent is heterozygous for this trait. Male marker EACA.MCTG32, for example, is linked in coupling with deep eyes. In contrast, no markers from the female parent were correlated with eye depth, so the female parent appears to be homozygous. Since the heterozygous male parent is deep-eyed, deep eyes must be dominant over shallow.

To search for possible modifiers, we tested for correlation between eye depth and all AFLP marker alleles not located on chromosome 10. None of these markers was found to be significantly correlated with eye depth.

Verification of the map, using a different population

Family 12586 shares the male parent 08675-21 with family 12601, which was used to map *Eyd*. Family 12586 also showed segregation of both tuber shape and eye depth. Marker STM1106 was polymorphic in this population. Among 47 clearly deep-eye-tuber clones, 29 carried one allele of the STM1106 marker, while the remaining 18 clones possessed an alternative allele; among 41 clones with clearly shallow-eye tubers, 13 displayed the first STM1106 allele, while the remaining

Table 3 Primer pairs used for polymerase chain reaction and amplified fragment length polymorphism analyses for the markers placed on the genetic map

Marker[a]	Primer pair (F: forward; R: reverse)	Reference
CP105	F: 5′TGTAAAGACTACAAATGCAAACTCCC R: 5′GCCTCTGTCTTTGCTGAAAAGAACA	This study (CP105F is based on gi|22022119, CP105R based on gi|22022215 of Gebhardt et al. 2003)
CT125	F: 5′TCAATGGACTTTGGCTGAGAAC R: 5′ GCAATCATGATAGGCATTGA	This study (based on gi|2897308 of Ganal et al. 1998)
CT240	F: 5′ GACCTAAGACATTGAAGAAGG R: 5′ACAAGGGTATTGTTGTCCTCAATC	This study (based on gi|2897434 of Ganal et al. 1998)
STM0051	F: 5′-TACATACATACACACACGCG R: 5′-CTGCAACTTATAGCCTCCA	Milbourne et al. 1998
STM1106	F: 5′-TCCAGCTGATTGGTTAGGTTG R: 5′-ATGCGAATCTACTCGTCATGG	Milbourne et al. 1998
EAAC.MCAG	EAAC with MCAG	Invitrogen
EACA.MCAC	EACA with MCAC	Invitrogen
EACA.MCTG	EACA with MCTG	Invitrogen
EACG.MCAA	EACG with MCAA	Invitrogen
EACT.MCAG	EACT with MCAG	Invitrogen
EACG.MCAT	EACG with MCAT	Invitrogen

[a]CP105, CT125, and CT240 primers were designed based on DNA sequences of the three RFLP probes of the same name. STM0051 and STM1106 are SSR markers. The rest are AFLP reaction sets

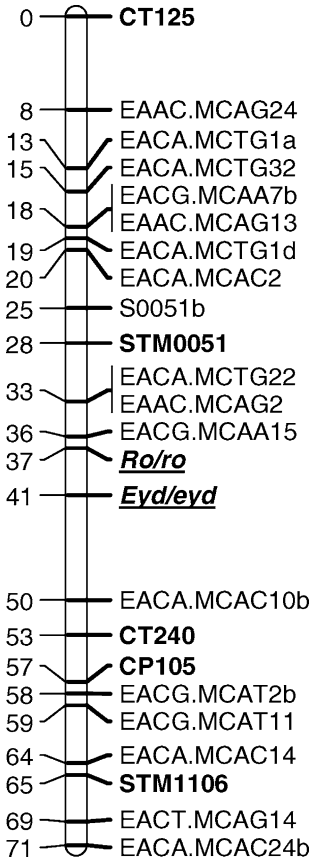

Fig. 2 Genetic map of potato chromosome 10 with the locations of the tuber shape (*Ro*/*ro*) and eye depth (*Eyd*/*eyd*) loci. *Ro*/*ro* Locus of the primary gene controlling tuber shape (*Ro* for round and *ro* for long), *Eyd*/*eyd* locus of the primary gene controlling tuber eye depth (*Eyd* for deep eyes, and *eyd* for shallow eyes). Markers in *boldface* are anchor markers known to be on chromosome 10. CT125, CT240, and CP105 are polymerase chain reaction (PCR)-based markers converted from the corresponding restriction fragment length polymorphism markers. STM0051 and STM1106 are simple sequence repeat markers. S0051b is a secondary marker detected by PCR analysis with STM0051 primers. The rest are amplified fragment length polymorphism markers

28 showed the alternative allele (data not shown). The results confirmed that *eyd* is linked to STM1106 ($P < 0.01$). The distance between *eyd* and STM1106 in family 12586 is thus approximately 35 cM, comparable to the distance of 24 cM (Fig. 2) observed in mapping family 12601.

Discussion

Phenotype

De Jong and Burns (1993) determined that a major gene, *Ro*, controls most of the variation between round and long tuber shapes. This gene has subsequently been mapped to chromosome 10 (Jacobs et al. 1995; van Eck et al. 1995). In the present paper, we determined that a major gene (tightly linked to *Ro*), *Eyd*, controls most of the variation of tuber eye depth. Although ideally no intermediate types (oval tuber shape and medium deep eyes) should occur, in practice (at least with the traits in question), this is not often achieved. The intermediate types may result from the major genes' interaction with one or more modifier genes.

Number of genes

Because of the reasons (small population, tetrasomic inheritance, and modifications by environmental factors) summarized in the "Introduction," the inheritance of eye depth of potato tubers is yet to be clarified. In our study, which included both classical genetic and molecular genetic mapping experiments, we unambiguously demonstrated that there is a major gene responsible for the eye depth trait. This observation is in agreement with Von Rathlef and Siebeneick (1934) and Maris (1962). We observed a few clones with intermediate type in eye depth, suggesting the existence of one or more modifying factors, which may explain why Huber (1930) proposed more than one gene controlling the trait.

Linkage between eye depth and tuber shape loci

The mapping results in the present study clearly demonstrated that the major locus (*Eyd*/*eyd*) of eye depth is linked with the major locus (*Ro*/*ro*) of tuber shape, and that the parents 11379-03 and 08675-21 have *roro* and *Roro* genotypes, respectively. While a LOD larger than 3 in the analysis of JoinMap may be sufficient for claiming a strong linkage between two loci, the linkage LOD score between the *Ro*/*ro* and *Eyd*/*eyd* loci eventually reached 22. This LOD score strongly supports the postulation (Maris 1962, 1966) that there is one major locus for eye depth, and that this locus is linked with the *Ro*/*ro* locus. The close linkage between the two loci may create difficulty in distinguish the two loci in some potato materials, which could explain why Von Rathlef and Siebeneick (1934) suggested it was a single major gene that controls both eye depth and tuber shape. The present study, however, demonstrated that *Ro* and *Eyd* are distinct loci, albeit tightly linked, located approximately 4 cM apart.

Dominant phenotype

Which phenotype, deep or shallow eye depth, is dominant? Although a century long effort, this question seems to be still in debate. East (1910) thought that the shallow eye phenotype is probably dominant over deep; Salaman (1911), Nilsson (1913), and Huber (1930) suggested that the deep eye phenotype is dominant; and Black (1930) proposed that neither allele is dominant and that the intermediate is heterozygous. In our present

study, if we considered only the data for eye depth, either deep or shallow could be dominant. However, when we analyzed eye depth jointly with tuber shape and coupling phase markers, it became clear that deep eye phenotype is dominant.

Breeding for tuber shape and eye depth

It is sometimes difficult to manipulate eye depth in breeding programs, in part because of tetrasomic inheritance, and in part because the trait can be influenced by environment. The results obtained in this study should provide breeders of cultivated tetraploid *S. tuberosum* with a better understanding of the genetics of the traits in question. This in turn can lead to greater efficiency in the breeding process. Using molecular markers linked to *Eyd* may also prove useful in selecting parents with lower dosage of deep eye alleles.

Conclusion

Results in the present study led to the following conclusions: (1) there is a major locus controlling the eye depth trait; (2) deep eye (*Eyd*) is dominant to shallow (*eyd*); (3) the *Eyd*/*eyd* locus is located on chromosome 10; and (4) the *Eyd*/*eyd* locus is closely linked with tuber shape *Ro*/*ro* locus, about 4 cM apart.

Acknowledgements The authors thank Drs. S. Tanksley, Cornell University, and C. Gebhardt, Max Planck Institute, for kindly providing anchor marker clones for chromosome 10. We thank Dr. Richard Tarn, Agnes Murphy, Valerie Burns and Ken Paddock as well as the greenhouse staff at the Potato Research Centre and the staff of the Benton Ridge Potato Breeding Substation for maintaining the potato clones. The scientific discussions with Dr. George Tai are much appreciated. We also thank Jiazheng (John) Yuan, Muhammad Haroon, Birt Stevens, Tieling Zhang, and Dr. Kerry Ready for technical assistance in nucleotide sequencing and in testing the segregation of molecular markers in the population 12601.

References

Black W (1930) Notes on the progenies of various potato hybrids. J Genetics 22:27–43

Bonierbale MW, Plaisted RL, Tanksley SD (1988) RFLP maps based on a common set of clones reveal modes of chromosomal evolution in potato and tomato. Genetics 120:1095–1103

De Jong H (1987) Inheritance of pigmented tuber flesh in cultivated diploid potatoes. Am Potato J 64:337–343

De Jong H, Burns VJ (1993) Inheritance of tuber shape in cultivated diploid potatoes. Am Potato J 70:267–283

De Jong H, Kawchuk LM, Burns VJ (1998) Inheritance and mapping of a light green mutant in cultivated diploid potatoes. Euphytica 103:83–88

East EM (1910) Inheritance in potatoes. Am Naturalist 44:424–430

Eck HJ van, Jacobs JM, Stam P, Ton J, Stiekema WJ, Jacobsen E (1994) Multiple alleles for tuber shape in diploid potato detected by qualitative and quantitative genetic analysis using RFLPs. Genetics 137:303–309

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

Feistritzer W (1952) Die Selbstunganalyse, eine Voraussetzung für die Kreuzungszucht der Kartoffel (Progeny analysis from selfing, a prerequisite for potato breeding). Z Pflanzenzuecht 31:173–195

Ganal MW, Czihal R, Hannappel U, Kloos DU, Polley A, Ling HQ (1998) Sequencing of cDNA clones from the genetic map of tomato (*Lycopersicum esculentum*). Genome Res 8:842–847

Gebhardt C, Ritter E, Barone A, Debener T, Walkemeier B, Schachtschabel U, Kaufmann H, Thompson RD, Bonierbale MW, Ganal MW, Tanksley SD, Salamini F (1991) RFLP maps of potato and their alignment with the homoeologous tomato genome. Theor Appl Genet 83:49–57

Gebhardt C, Mugniery D, Ritter E, Salamini F, Bonnel E (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, Walkemeier B, Henselewski H, Barakat A, Delseny M, Stuber K (2003) Comparative mapping between potato (*Solanum tuberosum*) and *Arabidopsis thaliana* reveals structurally conserved domains and ancient duplications in the potato genome. Plant J 34:529–541

Huber JA (1930) Genetische Versuche mit Salatkartoffeln (Genetic experiments with salad potatoes). Z Zuecht, Serie A, Pflanzenzuecht 15:75–85

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

Li XQ, Zhang M, Brown GG (1996) Cell-specific expression of mitochondrial transcripts in maize seedlings. Plant Cell 8:1961–1975

Maris B (1962) Analyse van aardappelpopulaties ten dienste van de veredeling (Analysis of potato populations as an aid in breeding). Doctoral Thesis, Agricultural University, Wageningen, p 208

Maris B (1966) The modifiability of characters important in potato breeding. Euphytica 15:18–31

Milbourne D, Meyer RC, Collins AJ, Ramsay LD, Gebhardt C, Waugh R (1998) Isolation, characterisation and mapping of simple sequence repeat loci in potato. Mol Gen Genet 259:233–245

Nilsson HN (1913) Potatis förädling och potatis bedömning (Breeding and evaluation of the potato). W Weibulls lrsbok 8:4–31. Abstract (in German) in Z Pflanzenzuecht 1:240–242 (1939)

Rathlef H von, Siebeneick H (1934) Über einige Kreuzungen peruanischer Sorten von *Solanum andigenum* Juz. et Buk mit Richters Jubel und die Genetik von Schalenfarbe, Knollenfarbe, Fleischfarbe, Blütenfarbe und Knollenform bei der Kartoffel (On some crosses of Peruvian sorts of *Solanum andigenum* Juz. et Buk. with Richters Jubel and the genetics of colour of skin, tuber, flesh and flower colour and of tuber shape in the potato). Genetica 16:153–176

Salaman RN (1911) The inheritance of colour and other characters in the potato. J Genetics 1:7–46

Tanksley SD, Ganal MW, Prince JP, de Vicente MC, Bonierbale MW, Broun P, Fulton TM, Giovannoni JJ, Grandillo S, Martin GB et al (1992) High density molecular linkage maps of the tomato and potato genomes. Genetics 132:1141–1160