

Assessment of genetic diversity and relatedness in the Latvian potato genetic resources collection by DArT genotyping

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Received 24 February 2015; Revised 17 June 2015; Accepted 10 July 2015 – First published online 14 August 2015

Abstract

Potato (*Solanum tuberosum* L.) has been cultivated in Latvia since the 17th century, and formal breeding programmes have been established since the start of the 20th century. The Latvian potato genetic resource collection consists of 83 accessions of Latvian origin, including landraces, old cultivars released starting from the 1930's, modern cultivars and breeding material. These are maintained in field and *in vitro* collections. Pedigree information about the potato cultivars is often limited, and the use of hybrids of local cultivars as parents is common in the Latvian potato breeding programme. Ninety-four Latvian potato varieties and breeding lines and some commonly used foreign accessions were genotyped with the potato DNA diversity array technology. Analysis of the Latvian potato genetic resources collection revealed that the amount of genetic diversity has increased in the modern cultivars in comparison with the old cultivars.

Keywords: breeding; DArT; diversity; fingerprinting; genetic resources; potato

Introduction

Potato (*Solanum tuberosum* L.) breeding has been undertaken in Latvia since the start of the 20th century, and locally developed cultivars have been available since the 1930's (Skrabule and Bebre, 2013). In the 1970's, the Latvian potato breeding programme was expanded, and additional germplasm was introduced from the Vavilov Plant Production Institute, Russia. In the Latvian potato breeding programme, increasing emphasis has been placed on quality traits (Murniece *et al.*, 2011) and organic farming conditions (Skrabule, 2010). Potato variety trials and breeding have been undertaken at the State Priekuli Plant Breeding Institute (SPPBI) since its establishment in 1913; however,

varieties have been developed in other agricultural institutions, as well as by the breeder A. Saulitis, who has utilized mutagenesis breeding (Skrabule and Bebre 2013). The Latvian potato genetic resources collection consists of 83 accessions of Latvian origin, including landraces, cultivars and breeding material. These are maintained in field and *in vitro* collections by the SPPBI.

Cultivated potato is a clonally propagated autotetraploid species, and has been characterized by using various DNA marker techniques (Milbourne *et al.*, 1997; McGregor *et al.*, 2000). Owing to the tetraploid genome, genotyping data are often analysed in a binary manner, which negates the advantages of using co-dominant marker systems such as simple sequence repeat (SSR) markers (Provan *et al.*, 1996; Milbourne *et al.*, 1997; Braun and Wenzel, 2005).

The DNA diversity array technology (DArT) is a microarray-based molecular marker system (Jaccoud *et al.*, 2001) that has been successfully applied for genetic

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diversity studies, linkage and association mapping in many different plant species (Wenzl *et al.*, 2004; Comadran *et al.*, 2009; Tyrka *et al.*, 2011; Alheit *et al.*, 2012; He and Bjørnstad, 2012). The DArT marker technique yields dominant marker genotypes, with a high multiplex ratio. This marker technique has been utilized for genetic mapping of resistance traits in potato (Śliwka *et al.*, 2012), as well as assessment of genetic diversity in wild potato accessions (Traini *et al.*, 2013).

The aim of this study was to investigate the genetic diversity and relatedness of Latvian potato genetic resources, by comparing old and modern cultivars, breeding material and foreign accessions that were utilized within the Latvian potato breeding programme.

Materials and methods

All potato accessions were obtained from the SPPBI collection. The majority were Latvian bred cultivars and foreign cultivars or breeding clones, but only one landrace was analysed ('Jelgavas Baltie') (Table S1, available online). The release dates of the cultivars were ranged from 1931 to 2010. The Latvian cultivars were predominantly developed in breeding programmes at the SPPBI or other breeding institutions and by the private breeder A. Saulitis (Table S1, available online). Genomic DNA was extracted from fresh leaves or sprout material using the Qiagen Plant DNA Minikit (Qiagen, Germany).

DArT marker genotyping was carried out by Diversity Arrays Technology Pty. Ltd., Canberra, Australia (<http://www.diversityarrays.com/>). Ninety-four potato accessions were genotyped with the potato DArT array producing 2762 loci. In total, 1482 DArT markers with two or less missing data points were retained after the quality control accounting for 139,308 genotypes including 0.8% of missing data points.

Inter primer binding site (iPBS) genotyping on the cultivars 'Spidola', 'SPO-11', 'Laima' and 'Priekulu Baltie' was performed as described previously by Kalendar *et al.* (2010), using 20 iPBS primers (2075, 2076, 2077, 2078, 2079, 2080, 2081, 2083, 2094, 2097, 2098, 2270, 2271, 2272, 2273, 2274, 2276, 2277, 2278 and 2279).

Analysis of the DArT genotypes was carried out by using dominant binary data. Polymorphism information content (PIC) values were calculated as $PIC = 1 - (p^2 + q^2)$, where p = fragment frequency and q = no fragment frequency (Nei, 1973). Genetic diversity analyses were performed with GenAEx 6 version (Peakall and Smouse, 2006) and DARwin (Perrier and Jacquemoud-Collet, 2006). Pair-wise genetic distances among cultivars were calculated from the binary data using Jaccard's coefficient, and dendrograms were constructed using the weighted Neighbour joining method. The robustness of the

dendrograms was examined by bootstrapping analysis (1000 bootstraps). The dendrogram was visualized by using the FigTree 1.4.2. program. Differences in pair-wise genetic distances and PIC values were compared by using Welch's *t*-test for unequal variances between groups.

DNA sequences of DArT clones polymorphic between cultivars 'Laima' and 'Priekulu Baltie' were obtained from Dr. A. Kilian (Diversity Arrays Technology Pty. Ltd., Canberra, Australia). BLASTN and BLASTX analyses against National Centre for Biotechnology Information GenBank nucleotide and non-redundant protein databases, respectively, were carried out on the NCBI website (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>) on 28 December 2014.

The potato cultivars were characterized according to the Latvian potato descriptor list (<http://www.genres.lv/en/kulturaugi/deskriptori/>) at the SPPBI in the years 2007–2009.

Results

Ninety-four Latvian potato varieties and breeding clones, and some commonly used foreign accessions were genotyped with the potato DArT array (Śliwka *et al.*, 2012), obtaining genotypes from 2762 DArT loci. After the quality control, 1482 DArT loci with two or less missing data points were retained for further analysis. All of the 1482 DArT loci were polymorphic in the full set of 94 analysed potato accessions, although 62 markers had a minor allele frequency less than 0.05. The PIC values ranged from 0.02 to 0.50, the maximum PIC value for dominant marker data (average 0.335, SD 0.138). Jaccard's genetic distances ranged from 0.001 to 0.632, average 0.510, SD 0.051. The DArT marker technique was able to distinguish all the analysed cultivars. Previously, a subset of the Latvian potato genetic resources collection was genotyped with eight SSR markers, and two pairs of cultivars could not be distinguished: 'Spidola' – 'SPO-11' and 'Laima' – 'Priekulu Baltie' (Zhuk *et al.*, 2008). Using the smaller 1482 locus set, and excluding missing data points in one or both pairs, the cultivars 'Spidola' and 'SPO-11' were differentiated at 24 DArT loci (from a total of 1448 loci – 1.66%), while the cultivars 'Laima' and 'Priekulu Baltie' were differentiated at only one DArT locus (from 1457 loci – 0.06%). When the full set of 2762 DArT loci was used to compare these two pairs of cultivars (again excluding missing data points in one or both pairs), there were 88 differences between 'Spidola' and 'SPO-11' (from a total of 2544 loci – 3.46%) and 9 differences between 'Laima' and 'Priekulu Baltie' (from 2602 loci – 0.35%). As clear phenotypic differences are observed between 'Laima' and 'Priekulu Baltie', the sequence homology-based annotation of polymorphic DArT marker clones was done between them by using

the BLASTN and BLASTX analyses to identify potential candidate genes (Table S2, available online). The DARt marker sequences were homologous to a range of genes/proteins, including a cytochrome P450 protein, an RGA-3-like resistance protein, starch synthase, a CMP-sialic acid transporter 4-like protein, a pentatricopeptide repeat-containing protein, a transcriptional regulatory protein and three uncharacterized sequences.

To confirm the polymorphism between both these pairs of cultivars, they were fingerprinted using an alternative marker method – iPBS, a retrotransposon based marker technique (Kalendar *et al.*, 2010). A total of 20 iPBS primers were utilized, and the primer 2075 detected a polymorphic fragment approximately 1300 bp in size between the cultivars ‘SPO-11’ and ‘Spidola’, while the primers 2080 and 2081 detected polymorphic fragments approximately 520 bp in size between the cultivars ‘Laima’ and ‘Priekulu Baltie’, confirming the genetic differentiation of these pairs of cultivars (Fig. 1).

From the cultivar characterization and evaluation trial results (2007–2008), tuber eye depth was assessed as very deep to deep for the cultivar ‘Laima’, but was

assessed deep to shallow for the cultivar ‘Priekulu Baltie’. A difference between tuber shape indexes for both cultivars was observed, but the difference was not significant ($P > 0.05$). The eye depth was deeper for the cultivar ‘Laima’ with round oval tubers than for the cultivar ‘Priekulu Baltie’ with oval tubers. Tubers of the cultivar ‘Laima’ were more resistant to internal bruising than ‘Priekulu Baltie’ tubers. The tuber flesh enzymatic darkening in the cultivar ‘Laima’ was very weak, but was more pronounced in the cultivar ‘Priekulu Baltie’. Internal bruising and tuber flesh discoloration is less pronounced for round tubers than for oval or long oval tubers (Molema *et al.*, 1997a, b), which was noted in this case with the cultivar ‘Laima’. The tuber flesh enzymatic darkening is caused by oxidation of phenols. This trait appears to be a dominant character governed by small number of genetic factors (Dale and Mackay, 1994). Less enzymatic activity was observed in the cultivar ‘Laima’ than in ‘Priekulu Baltie’ as tuber flesh darkening was very weak in this cultivar.

The potato accessions were divided into four groups – Latvian cultivars (32 accessions), Latvian breeding

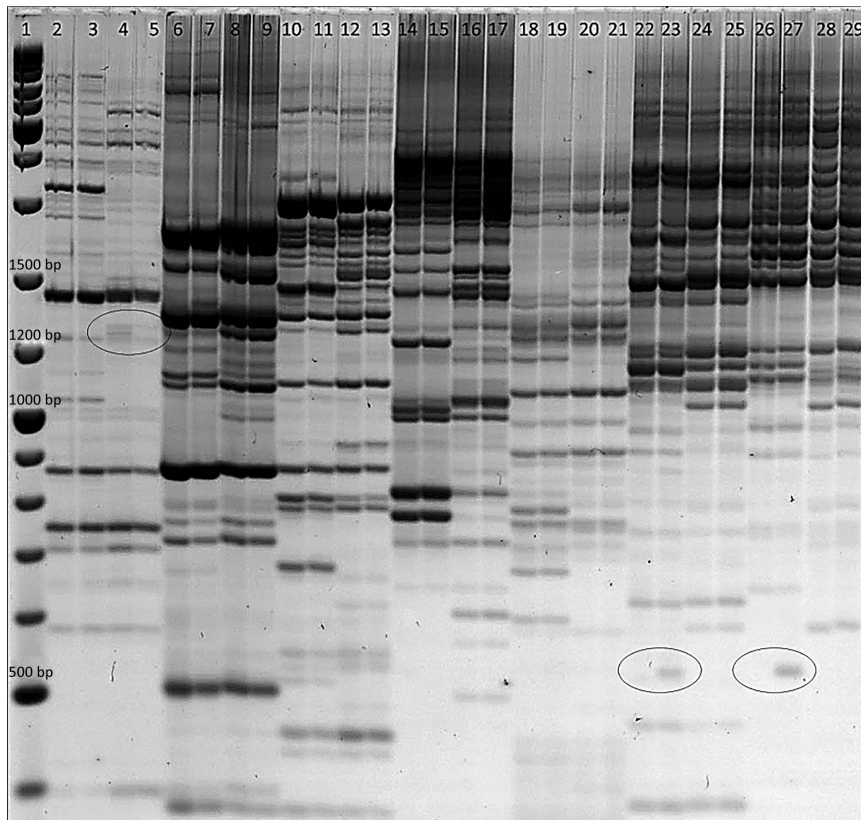


Fig. 1. iPBS marker genotyping of the cultivars ‘Laima’ (lanes 2, 6, 10, 14, 18, 22 and 26), ‘Priekulu Baltie’ (lanes 3, 7, 11, 15, 19, 23 and 27), ‘Spidola’ (lanes 4, 8, 12, 16, 20, 24 and 28) and ‘SPO-11’ (lanes 5, 9, 13, 17, 21, 25 and 29). iPBS markers: 2075 (lanes 2–5), 2076 (lanes 6–9), 2077 (lanes 10–13), 2078 (lanes 14–17), 2079 (lanes 18–21), 2080 (lanes 22–25) and 2081 (lanes 26–29). Differentially amplified fragments between cultivar pairs are circled. Lane 1 – size standard (GeneRuler DNA ladder mix (Thermo Fisher Scientific, Lithuania)).

Table 1. Genetic diversity parameters of breeding lines and Latvian cultivars, old and modern Latvian cultivars

	PIC (SD)	Genetic distance (SD)
Breeding clones	0.329 (0.143)	0.510 (0.057)
Latvian cultivars (all)	0.320 (0.156)	0.499 (0.076)
Old cultivars (prior to 1970)	0.264 (0.186)	0.435 (0.109)
Modern cultivars	0.326 (0.159)	0.523 (0.067)

materials (39 accessions), Western European cultivars (15 accessions) and Eastern cultivars (8 accessions). AMOVA indicated that only 2% of the genetic diversity was found between these groups ($P < 0.01$). The level of genetic diversity within the Latvian potato accessions was further examined, comparing the PIC values and pair-wise genetic distances within the cultivars and breeding material (Table 1). In the cultivars, 68 of the 1482 DArT markers were fixed ($F = 0$ or 1), and 59 markers were low frequency alleles ($F < 0.05$), while in the breeding material 20 DArT markers were fixed, and 61 markers were low frequency alleles ($F < 0.05$). The average PIC value in the cultivars was 0.320 (SD 0.156), and 0.329 (SD 0.143) in the breeding material, which was not significantly different. The pair-wise genetic distances were marginally lower between the cultivars (average 0.499, SD 0.076) than in the breeding material (average 0.510, SD 0.057); however, this difference was significantly different ($P = 0.003$).

The genetic diversity of old (<1970) and modern Latvian cultivars was compared. A total of 16 modern cultivars and 14 old cultivars could be unambiguously identified from the Latvian potato collection. In the modern cultivars, 131 of the 1482 DArT markers were fixed ($F = 0$ or 1), while in the old cultivar group 303 DArT markers were fixed. There were 143 unique DArT markers found only in the modern cultivars, and 29 markers found only in the old cultivars. The average PIC value of the 1482 DArT marker set was significantly lower in the old cultivars (0.264, SD 0.186) than in the modern cultivars (0.326, SD 0.159) ($P < 0.001$). The average pair-wise Jaccard's genetic distances were also significantly lower between the old cultivars (0.435, SD 0.109) compared with the modern cultivars (0.523, SD 0.067) ($P < 0.001$) (Table 1).

The dendrogram constructed using all accessions genotyped using the DArT markers was mostly consistent with the known pedigrees of the accessions (Fig. 2). All varieties developed by the breeder A. Saulitis (except for KPAX-11) clustered separately from the other accessions (the majority of which were developed by SPPBI). There was one well-supported cluster that contained the old varieties 'Laima', 'Priekulu Baltie', 'Agra',

'Eksports', 'Jubileja' and the landrace 'Jelgavas Baltie'. Otherwise, there was no separation of the Latvian varieties, breeding material and foreign cultivars. Breeding clones derived from the same cross clustered together, sometimes with one or both the parental cultivars (e.g. 95-36.100, 95-36.114, 95-36.133, 'Mandaga' and the parent cultivar 'Zarevo'; S01075-4, S01075-5, and the parent cultivar 'Dina'). Occasionally, some clones from the same cross clustered together with the parental cultivars, e.g. S01085-21, S01085-30, S01085-35, S01085-54 clustered with the parent cultivars 'Pepo' and 'Vineta'. In other cases, the breeding clone was clustered separately from both parental cultivars, e.g. (S00028-13, 'Zhukovskiy ranniy' and 'Dina').

Discussion

The DArT marker technique was an efficient method for genotyping the Latvian potato collection. The average PIC value in the analysed accessions was 0.335, which was similar to the average DArT marker PIC values found in other cultivated species, e.g. carrot 0.301 (Grzebelus *et al.*, 2014), rye 0.34 (Bolibok-Bragoszewska *et al.*, 2014), sorghum 0.410 (Mace *et al.*, 2008), barley 0.38 (Wenzl *et al.*, 2004), wheat and triticale 0.36 (Badea *et al.*, 2011) and hop 0.335 (Howard *et al.*, 2011). The DArT markers were able to distinguish the two pairs of accessions that could not be uniquely fingerprinted with the SSR markers. The cultivars 'Spidola' and 'SPO-11' were differentiated at 1.66–3.46% of the DArT marker loci. This rate is much higher than the previously reported maximum gamma ray induced mutation rate of less than one mutation per 1810 bp (0.05%) in tetraploid potato (Elias *et al.*, 2009), which indicating that the cultivar 'SPO-11' is most probably not an induced mutant derived from the cultivar 'Spidola'. More surprising was the low differentiation of the cultivars 'Laima' and 'Priekulu Baltie' (0.06–0.35%). According to pedigree data, 'Laima' is derived from a cross between 'Irish Cobbler' and 'Jubel', while 'Priekulu Baltie' is derived from a cross between 'Kameraz 18-368' and 'Agra', which itself is derived from 'Irish Cobbler'. The genetic differentiation of these two pairs of cultivars was verified by fingerprinting with an alternative marker technique – iPBS, which revealed a low level of overall genetic polymorphism between these pairs of cultivars, but identified differentially amplified iPBS fragments. In addition, these two pairs of cultivars also differ in several characterization and evaluation descriptors, particularly with regard to tuber and plant characteristics (Skrabule, unpublished).

The nine DArT markers that differentiate 'Laima' and 'Priekulu Baltie' were annotated by BLASTN and BLASTX analyses, which identifying candidate genes for the

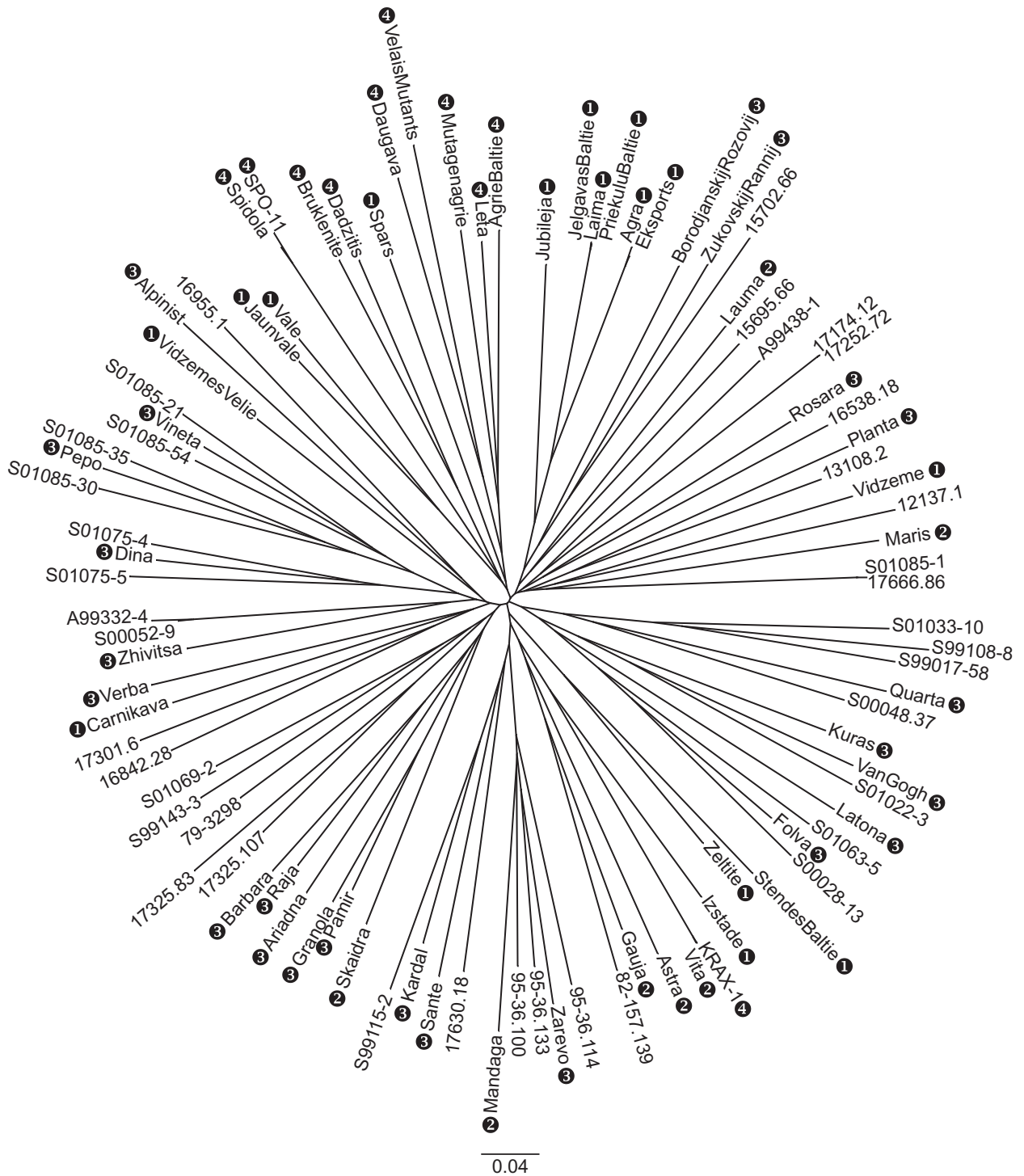


Fig. 2. Dendrogram of potato accessions based on 1482 DArT marker genotypes was visualized in FigTree 1.4.2. Old Latvian cultivars (1931–1970), new cultivars (1971–2010), foreign cultivars and A. Saulitis’ cultivars are numbered from one to four, respectively. The unnumbered accessions are Latvian breeding lines.

observed phenotypic differences (Table S2, available online). Further analyses of these candidate genes will enable the elucidation of the genetic basis of the observed phenotypic differences between these two cultivars.

There was a little genetic differentiation between the Latvian cultivars, breeding material and foreign (mostly European) cultivars, which reflecting the common provenance of the Latvian and European potato cultivars.

The breeding programme accessions include advanced clones, which were derived from the crosses between foreign cultivars with the aim of combining useful traits from parent cultivars. The assessment and selection of advanced breeding clones within the region of expected future deployment ensure that the clones containing unique combinations of genes from the cultivated potato gene pool, which are most adapted to local growing conditions, are advanced to cultivars. Thus, the local adaptive diversity of the potato germplasm pool is increased, and allows for the development of new cultivars adapted to local conditions.

Potato breeding has been carried out in Latvia since the start of the 20th century. Old Latvian potato cultivars were defined as those released prior to the 1970's, and genetic diversity between old and modern cultivars was examined. The genetic diversity parameters were lower in the old cultivars than in the modern cultivars. This could be due to the influx of new breeding germplasm into the Latvian breeding programme that occurred in the 1970's. This in turn is a reflection of the increasing genetic diversity in potato breeding programmes resulting from the use of wild *Solanum* germplasm (Gebhardt *et al.*, 2004; Hajjar and Hodgkin, 2007), with the aim of introgressing resistance to pests or specific quality traits. This maintenance or even increase of genetic diversity in cultivars since the 1960's and 1970's has been reported for other crop species as well (van de Wouw *et al.*, 2010). All of the old cultivars did not cluster separately from the modern cultivars, suggesting that the combination of locally adapted cultivars with donors of specific resistance and other traits has been successful, and has increased the amount of genetic diversity within Latvian potato cultivars without causing a shift in the population away from locally adapted germplasm.

Analysis of the Latvian potato genetic resources collection has revealed that the amount of genetic diversity has increased in the modern cultivars in comparison with the old cultivars released prior to 1970, indicating that the Latvian potato breeding programme has successfully expanded the genetic base of Latvian potatoes, integrating this with locally adapted older varieties.

Supplementary material

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S14792621150003988>

Acknowledgements

The authors thank Ruslan Kalendar and Alan Schulman from the MTT/BI Plant Genomics Laboratory, Institute

of Biotechnology, Viikki Biocenter, University of Helsinki, for performing the iPBS genotyping of the cultivars 'Spidola', 'SPO-11', 'Laima' and 'Priekulu Baltie', and to Andrzej Kilian from the Diversity Array Technology Pty. Ltd, Canberra, Australia for DArT genotyping and for providing sequences of DArT clones. This research was supported by the State Research Programme in Agrobiotechnology (2006–2009) and the Programme for research, maintenance, reproduction and documentation of Latvia crop genetic resources financed by the Ministry of Agriculture.

References

- Alheit KV, Maurer HP, Reif JC, Tucker MR, Hahn V, Weissmann EA and Wurschum T (2012) Genome-wide evaluation of genetic diversity and linkage disequilibrium in winter and spring triticale (x *Triticosecale* Wittmack). *BMC Genomics* 13: 235. doi:10.1186/1471-2164-13-235.
- Badea AFE, Salmon D, Tuvešson S, Vrolijk A, Larsson C-T, Caig V, Huttner E, Kilian A and Laroche A (2011) Development and assessment of DArT markers in triticale. *Theoretical and Applied Genetics* 122: 1547–1560.
- Bolibok-Bragoszewska H, Targońska M, Bolibok L, Kilian A and Rakoczy-Trojanowska M (2014) Genome-wide characterization of genetic diversity and population structure in Secale. *BMC Plant Biology* 14: 184.
- Braun A and Wenzel G (2005) Molecular analysis of genetic variation in potato (*Solanum tuberosum* L.). I. German cultivars and advanced clones. *Potato Research* 47: 81–92.
- Comadran J, Thomas W, van Eeuwijk F, Ceccarelli S, Grandó S, Stanca A, Pecchioni N, Akar T, Al-Yassin A, Benbelkacem A, Ouabboh H, Bort J, Romagoas I, Hackey CA and Russell JR (2009) Patterns of genetic diversity and linkage disequilibrium in a highly structured *Hordeum vulgare* association-mapping population for the Mediterranean basin. *Theoretical and Applied Genetics* 119: 175–187.
- Dale MFB and Mackay GR (1994) Inheritance of table and processing quality. In: Bradshaw JE and Mackay GR (eds) *Potato Genetics*. Wallingford: CAB International, pp. 285–307.
- Elias R, Till B J, Mba C and Al-Safadi B (2009) Optimizing TILLING and ecotilling techniques for potato (*Solanum tuberosum* L.). *BMC Research Notes* 2: 141.
- Gebhardt C, Ballvora A, Walkemeier B, Oberhagemann P and Schuler K (2004) Assessing genetic potential in germplasm collections of crop plants by marker-trait association: a case study for potatoes with quantitative variation of resistance to late blight and maturity type. *Molecular Breeding* 13: 93–102.
- Grzebelus D, Iorizzo M, Senalik D, Ellison S, Cavagnaro P, Macko-Podgorni A, Heller-Uszynska K, Kilian A, Nothnagel T, Allender C, Simon PW and Baranski R (2014) Diversity, genetic mapping, and signatures of domestication in the carrot (*Daucus carota* L.) genome, as revealed by Diversity Arrays Technology (DArT) markers. *Molecular Breeding* 33: 625–637.
- Hajjar R and Hodgkin T (2007) The use of wild relatives in crop improvement: a survey of developments over the last 20 years. *Euphytica* 156: 1–13.

- He X and Bjørnstad Å (2012) Diversity of North European oat analyzed by SSR, AFLP and DArT markers. *Theoretical and Applied Genetics* 125: 57–70.
- Howard EL, Whittock SP, Jakše J, Carling J, Matthews PD, Probasco G, Henning JA, Darby P, Cerenak A, Javornik B, Kilian A and Koutoulis A (2011) High-throughput genotyping of hop (*Humulus lupulus* L.) utilising diversity arrays technology (DArT). *Theoretical and Applied Genetics* 122: 1265–1280.
- Jaccoud D, Peng K, Feinstein D and Kilian A (2001) Diversity arrays: a solid state technology for sequence independent genotyping. *Nucleic Acids Research* 29: e25.
- Kalendar R, Antonius K, Smýkal P and Schulman AH (2010) iPBS: a universal method for DNA fingerprinting and retrotransposon isolation. *Theoretical and Applied Genetics* 121: 1419–1430.
- Mace ES, Xia L, Jordan DR, Halloran K, Parh DK, Huttner E, Wenzl P and Kilian A (2008) DArT markers: diversity analyses and mapping in *Sorghum bicolor*. *BMC Genomics* 9: 26.
- McGregor CE, Lambert CA, Greyling MM, Louw JH and Warnich L (2000) A comparative assessment of DNA fingerprinting techniques (RAPD, ISSR, AFLP and SSR) in tetraploid potato (*Solanum tuberosum* L.) germplasm. *Euphytica* 113: 135–144.
- Milbourne D, Meyer R, Bradshaw JE, Baird E, Bonar N, Provan J, Powell W and Waugh R (1997) Comparison of PCR-based marker systems for the analysis of genetic relationships in cultivated potato. *Molecular Breeding* 3: 127–136.
- Molema GJ, Klooster JJ, Verwijs BR, Hendriks MMWB and Bretele H (1997a) Effect of impact body shape on subcutaneous tissue discoloration in potato tubers. *Netherlands Journal of Agricultural Science* 45: 407–421.
- Molema GJ, Verwijs BR, Van der Berg JV and Bretele H (1997b) Effect of repetitive impacts on subcutaneous tissue discoloration in potato tubers. *Netherlands Journal of Agricultural Science* 45: 187–200.
- Murniece I, Karklina D, Galoburda R, Santare D, Skrabule I and Costa HS (2011) Nutritional composition of freshly harvested and stored Latvian potato (*Solanum tuberosum*) varieties depending on traditional cooking methods. *Journal of Food Composition and Analysis* 24: 699–710.
- Nei M (1973) Analysis of gene diversity in subdivided populations. *Proceedings of the National Academy of Sciences* 70: 3321–3323.
- Peakall R and Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* 6: 288–295.
- Perrier X and Jacquemoud-Collet JP (2006) DARwin software. <http://darwin.cirad.fr/>
- Provan J, Powell W and Waugh R (1996) Microsatellite analysis of relationships within cultivated potato (*Solanum tuberosum*). *Theoretical and Applied Genetics* 92: 1078–1084.
- Skrabule I (2010) Evaluation of potato breeding clones in organic and conventional growing conditions. In: *EUCARPIA 2nd Conference of the "Organic and Low-input Agriculture" Section*. Paris, pp. 102–105.
- Skrabule I and Bebre G (2013) Development of potato varieties in Latvia. *Proceedings of the Latvian Academy of Science* 67: 296–301.
- Śliwka J, Jakuczun H, Chmielarz M, Hara-Skrzypiec A, Tomczyńska I, Kilian A and Zimnoch-Guzowska E (2012) A resistance gene against potato late blight originating from *Solanum × michoacanum* maps to potato chromosome VII. *Theoretical and Applied Genetics* 124: 397–406.
- Traini A, Iorizzo M, Mann H, Bradeen JM, Carputo D, Frusciantone L and Chiusano ML (2013) Genome microscale heterogeneity among wild potatoes revealed by diversity arrays technology marker sequences. *International Journal of Genomics* 2013: 257218. doi:10.1155/2013/257218.
- Tyrka M, Bednarek PT, Kilian A, Wedzony M, Hura T and Bauer E (2011) Genetic map of triticales compiling DArT, SSR, and AFLP markers. *Genome* 54: 391–401.
- van de Wouw M, van Hintum T, Kik C, van Treuren R and Visser B (2010) Genetic diversity trends in twentieth century crop cultivars: a meta analysis. *Theoretical and Applied Genetics* 120: 1241–1252.
- Wenzl P, Carling J, Kudrna D, Jaccoud D, Huttner E, Kleinhofs A and Kilian A (2004) Diversity Arrays Technology (DArT) for whole-genome profiling of barley. *Proceedings of the National Academy of Sciences USA* 101: 9915–9920.
- Zhuk A, Veinberga I, Skrabule I and Rungis D (2008) Characterization of Latvian potato genetic resources by DNA fingerprinting with SSR markers. *Agronomijas Vestis* 11: 171–178.