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The United States Potato Genebank Holding of cv. Desiree is a Somatic Mutant of cv. Urgenta

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Abstract

Genome-wide markers enable routine confirmation of whether varieties are true-to-type, and when they are not, to infer their identity. The objective of this study was to determine the basis of a previously described chromosome translocation, tr8-7, which was apparently polymorphic among holdings of the tetraploid potato (*Solanum tuberosum* L.) cultivar Desiree. Through analysis of publicly available genotype data from North American and European tetraploid potato germplasm, we resolved a longstanding mistaken identity of the United States Potato Genebank holding of Desiree, which is actually a somatic mutant of its maternal parent, cv. Urgenta. Comparison of multiple holdings revealed that tr8-7 was a somatic mutation that occurred at least 25 years ago and was maintained in isolated lineages. Holdings from other institutions lacked tr8-7 and were confirmed as Desiree by trio analyses, suggesting that the mixup affected the United States Potato Genebank and institutions that received Desiree from there. In the face of inevitable mutations and human error, we recommend validation of potato germplasm collections with pedigree and genomic information. To that effect, we provide molecular markers to distinguish the varieties investigated in this study.

Resumen

Los marcadores de todo el genoma permiten la confirmación rutinaria de si las variedades son fieles al tipo, y cuando no lo son, inferir su identidad. El objetivo de este estudio fue determinar la base de una translocación cromosómica previamente descrita, tr8-7, que aparentemente era polimórfica entre las particularidades de la variedad tetraploide de papa (*Solanum tuberosum* L.) Desiree. A través del análisis de datos de genotipos disponibles p(iblicamente del germoplasma tetraploide de papa de América del Norte y Europa, resolvimos una identidad errónea de largo tiempo de las particularidades de Desiree del Banco de Germoplasma de la Papa de los Estados Unidos, que en realidad es un mutante somático de su progenitor materno, cv. Urgenta. La comparación de m(iltiples particularidades reveló que tr8-7 era una mutación somática que ocurrió hace al menos 25 años y se mantuvo en linajes aislados. Las particularidades de otras instituciones carecían de tr8-7 y fueron confirmadas como Desiree por análisis triples, lo que sugiere que la confusión afectó al Banco de Germoplasma de la Papa de los Estados Unidos y a las instituciones que recibieron Desiree de allí. Ante las mutaciones inevitables y el error humano, nosotros recomendamos la validación de las colecciones de germoplasma de papa con pedigrí e información genómica. Para ello, proporcionamos marcadores moleculares para distinguir las variedades investigadas en este estudio.

Keywords Trio analysis · Clone identification · SNP array · Genome sequencing · Breeding · Clone · Chromosome translocation · Somatic evolution

Introduction

As a clonal crop and a facultatively clonal wild species, potatoes undergo prolonged vegetative growth and, over time, accumulate somatic mutations. Many important cultivars have been grown, propagated and distributed globally for decades. Recently, a concerted effort has been made to genotype diverse potato germplasm using SNP arrays

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(Hirsch et al. 2013; Vos et al. 2015; Endelman et al. 2017; Ellis et al. 2018; Sharma et al. 2018; Prodhomme et al. 2020; Pandey et al. 2021), whole-genome resequencing (Uitdewilligen et al. 2013; Hardigan et al. 2017; Pham et al. 2017; Li et al. 2018) or genome assembly (Tang et al. 2022). These datasets offer rich resources to investigate potato genome evolution, revealing high levels of genomic diversity and rampant structural variation (Hardigan et al. 2016, 2017; Zhou et al. 2020; Bao et al. 2022; Hoopes et al. 2022; Sun et al. 2022; Tang et al. 2022). They also enable discovery and correction of pedigree errors (Endelman et al. 2017; Pandey et al. 2021). By comparing multiple holdings of the same cultivar, changes to potato genomes can be placed in the context of their propagation and distribution history.

Desiree is a selection of Urgenta x Depesche that was released by the Dutch potato breeding company HZPC in 1962. It is now held by at least ten stock centers around the world (Genesys 2022). As it is responsive to tissue culture regeneration (Ooms et al. 1987; Stiekema et al. 1988), it has been a standard cultivar for research using transgenic (McCue et al. 2005; Van Eck et al. 2007; Pieczynski et al. 2013; Haesaert et al. 2015; Jahan et al. 2015; Ghislain et al. 2019) and genome-edited potatoes (Nicolia et al. 2015; Butler et al. 2016; Craze et al. 2018; Veillet et al. 2019, 2020; Gonzalez et al. 2020). Previous research has hinted at somatic variation among holdings of cv. Desiree. We recently showed that the USPG Desiree holding carried an unbalanced translocation, tr8-7 (Comai et al. 2021). Specifically, individuals with tr8-7 carry a fifth copy of a terminal 5.6 Mb chromosome 7 segment instead of the terminal 4.6 Mb on one of the chromosome 8 homologs. In contrast, Desiree holdings from either Cornell University or the International Potato Center (CIP) did not appear to carry tr8-7 (Fossi et al. 2019; Amundson et al. 2021). This could be due to somatic variation among Desiree clones, or alternatively, that some clones were mistyped.

To understand the basis of apparent tr8-7 variation among Desiree holdings, we compared the genomes of six holdings from genebanks and laboratories throughout the United States and Europe. We asked three questions. First, which holdings carry tr8-7? Second, which holdings are truly Desiree? Third, if any of the holdings are not Desiree, what are they? Our objectives were to genotype each holding for tr8-7 polymorphism and to test the identity of each holding through analysis of parent–offspring trios.

Materials and Methods

Plant Material and Growth Conditions

In vitro cuttings of Desiree (PI310467) were acquired from the US Potato Genebank (USPG) in 2015, and from both the UC Davis Plant Transformation Facility (PTF) and the laboratory of Joyce Van Eck (Boyce Thompson Institute, Cornell University) in 2021. Cuttings of Urgenta (PI217560) were acquired from the USPG in 2021. All other Desiree holdings had been sequenced or array-genotyped in previous works. Single-node cuttings were grown in vitro under 16 h light 25 °C: 8 h dark 18 °C on half-strengt h Murashige and Skoog media adjusted to pH 5.7 with KOH and supplemented with 1% sucrose, 1 × Gamborg vitamins and 0.5 g/L MES buffer. Individual nodes were transferred to fresh media every 1–2 months.

Library Preparation and Sequencing

Genomic DNA was extracted from leaves of in vitro grown plants as previously described (Ghislain et al. 1999). Approximately 750 ng of genomic DNA was used as input with a KAPA Hyper Prep Kit (Roche, Switzerland) with half-scale reactions as previously described (Amundson et al. 2020). Libraries were sequenced on an Illumina NovaSeq 6000 instrument at the University of California San Francisco Center for Advanced Technologies. Sequencing reads were demultiplexed using allprep-12.py, a custom Python script available at https://github. com/Comai-Lab/allprep. Previously generated genomic sequence reads of PI310467 (Comai et al. 2021), CIP Desiree (Amundson et al. 2021), BrACySol Desiree (Sevestre et al. 2020), and panels of mainly North American cultivars (Hardigan et al. 2017; Pham et al. 2017) were retrieved from the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) and incorporated in subsequent analyses.

Sequence Data Analysis

Short read sequences were processed as described previously (Amundson et al. 2020). Briefly, adapter and low-quality sequence were trimmed from raw reads with cutadapt (version 1.15) (Martin 2011). Trimmed reads were aligned to DM1-3 v6. 1 reference assembly (Pham et al. 2020) using BWA MEM (version 0.7.12-r1039) and default parameters. PCR duplicates were marked with the MarkDuplicates function of Picard (version 2.18), and one mate of an overlapping read pair was soft-clipped using ClipOverlap from bamutils (version 1.0.14) (Breese and Liu 2013). Read depth at each position of the reference genome was obtained by running samtools depth -a on each processed BAM file. Median read depth in non-overlapping 10 kb windows was calculated with bedtools map (version 2.2.27) (Quinlan and Hall 2010) and shown in coverage plots.

Genotype Data Consolidation

We consolidated SNP array data from four studies (Hirsch et al. 2013; Endelman et al. 2017; Sharma et al. 2018; Prodhomme et al. 2020). in the following way.

Supplemental Table S4 from (Hirsch et al. 2013) describes allele dosage calls for 250 lines (2 monoploid, 27 diploid and 221 tetraploid) of the SolCAP diversity panel at 3,763 SNP loci. The genotype data were obtained using the Infinium 8 k Potato SNP (Felcher et al. 2012). Genotype calls in this dataset were formatted as base calls. For example, a biallelic SNP could be either CCCC, CCCT, CCTT, CTTT or TTTT for a tetraploid, and either CC, CT or TT for a diploid. Genotype calls of DM1-3, which corresponded to the reference genome, were included.

The dataset provided by Endelman et al. (2017) includes 109 samples from the Hirsch et al. (2013) dataset and an additional 207 samples. Genotype calls were formatted as allele count in the range [0,4] and DM1-3 was not included.

Supplemental Table S10 from (Sharma et al. 2018) included allele dosage calls of 340 tetraploid lines at 5,718 SNPs, also obtained using the Infinium 8 k SNP array (Felcher et al. 2012). Genotype calls were formatted as tetraploid allele dosage, with base calls formatted as AAAA, AAAB, AABB, ABBB or BBBB at each SNP. Although DM1-3 was genotyped in the study, its calls were not included in the dataset.

Finally, supplemental Table S1 from (Prodhomme et al. 2020) included allele dosage calls of 330 tetraploid lines genotyped at 10,968 SNP loci with the PotVar V1 SNP array, which includes both the Infinium 8 k SNPs and candidate SNPs identified by (Uitdewilligen et al. 2013). This dataset was a subset of the genotype data reported by (Vos et al. 2015), but the genotype data themselves were not available from the publication. Genotype calls were formatted as minor allele count in the range [0,4] and DM1-3 was not included.

We first joined the datasets from Hirsch et al. (2013) and Endelman et al. (2017). Using the 109 varieties represented in both datasets, we derived a consensus definition of each allele at each SNP. At a single locus, for example, a variety showing genotype "1" at a locus in the Endelman dataset and "TTTC" in the Hirsch dataset support that the numeric genotypes represent the dosage of the C allele. For most loci, the consensus alleles were strongly supported. After removing duplicate entries, the combined Hirsch and Endelman dataset contained genotype calls for 429 samples at 3,740 SNPs.

In this same manner, we converted the A vs. B genotype calls of the Prodhomme dataset to base calls, using the consensus of 11 varieties shared between the Prohomme and Hirsch datasets: Bintje, Defender, Early Rose, Katahdin, Kennebec, Ranger Russet, Russet Burbank, Spunta, Stirling, Umatilla Russet and Yukon Gold. Similarly, the identities of the "A" and "B" alleles of the Sharma dataset were converted to base calls using the consensus of 16 varieties shared between the Sharma and Hirsch datasets: Atlantic, Bintje, Chieftain, Dark Red Norland, Defender, Kennebec, Ranger Russet, Red Pontiac, Russet Burbank, Russet Norkotah, Sierra Gold, Spunta, Stirling, Superior, Torridon and Umatilla Russet.

To merge array and sequence-based genotypes, variants were identified from each sequenced variety using freebayes (version 1.3.1) with 2,067 SNPs from the consolidated array genotypes provided as targets. The following parameters were also specified: read mapping quality ≥ 20, base quality ≥ 20, Hardy–Weinberg priors off, and haplotype length -1. Variants were changed from 0/1 REF/ALT notation to base calls and merged with the array genotypes. For each locus, if DM1-3 array and sequencing base calls were reverse complements of each other, the array genotypes were reverse-complemented. All genotypes were then converted to counts of the reference allele, as reported in the VCF output. The R code developed to consolidate the genotype datasets is provided as Supplemental File S1, and the consolidated dataset including all array and sequence-based genotype calls, is provided as Supplemental File S2.

Phylogenetic Methods

A neighbor joining tree was constructed from pairwise Euclidean distances in R using the phangorn package in R version 3.6.2. Average pairwise identity by state between pairs of tetraploid samples was calculated as:

$$IBS_{(a,b)} = \frac{1}{4n}\sum_{i=1}^{n} Sim(g_{ai}, g_{bi})$$

where $Sim_{(gai,gbi)}$ was 0 if genotypes a and b shared no alleles at the SNP at hand, 1 if one allele was shared, 2 if two alleles were shared, 3 if three alleles were shared and 4 if four alleles were shared. For plotting, samples were clustered using hclust() with the "complete" agglomeration method in R version 3.6.2.

PCR Markers

Primer combinations are listed in Supplemental Table S5. All reaction conditions were 20 ng template DNA and 0.25 µM each primer and 1X GoTaq Green Master Mix (Promega, USA) in a 10 µl reaction volume. For amplification of the tr8-7 junction, reactions were held at 95 °C for 3 min, 35 cycles of 95 °C for 30 s, 59 °C for 30 s, 72 °C for 1 min, and a final extension at 72 °C for 5 min. Junction PCR products were separated on a 1% agarose gel. Sanger sequencing of the PCR product from the USPG Desiree holding was performed by the UC Davis DNA Sequencing Facility. For CAPS markers, 20 ng of genomic DNA was

used as a template in 50 µl reactions with 0.25 µM of each primer and 1 × GoTaq Green Master Mix (Promega, USA). Reactions were held at 95 °C for 3 min, 35 cycles of 95 °C for 30 s, 58 °C for 30 s, 72 °C for 30 s, and a final extension at 72 °C for 5 min. Products were cleaned with 1.8 × volumes of Seramag Speedbeads (Cytiva, UK) according to manufacturer's protocol and eluted in 20 µl 10 mM Tris–HCl, pH 8.0. Approximately 100 ng of each PCR product was digested with 1 unit of BamHI-HF (New England Biolabs, USA) in 1X CutSmart buffer in a 10 µl reaction volume at 37 °C overnight. Restriction products were separated on a 1.5% agarose gel.

Results

Phenotypic Description of Desiree Holdings

Phenotypically, USPG Desiree and the Cornell Desiree were very similar, but there are a few distinguishing features (Fig. 1). Leaf morphology at the whole plant level was similar (Fig. 1a–b). Compared to Cornell Desiree, USPG Desiree showed darker purple color of flower petals, darker orange color of the anthers (Fig. 1c–d), and lighter red tuber skin (Fig. 1e–f). Both varieties showed yellow tuber flesh (Fig. 1g–h).

Desiree Holdings Differed By a Chromosome Translocation

To determine whether Desiree holdings other than USPG Desiree carried tr8-7, we compared whole-genome sequence data of five Desiree holdings: one each from Cornell University described above, the International Potato Center (CIP), INRA BrACySol Biological Resource Center (BrACySol), the University of California Davis Plant Transformation Facility (PTF) and USPG. The PTF stock of Desiree was acquired from the USPG approximately 25 years ago (D. Tricoli, personal communication). The maternal parent of Desiree, cv. Urgenta, was

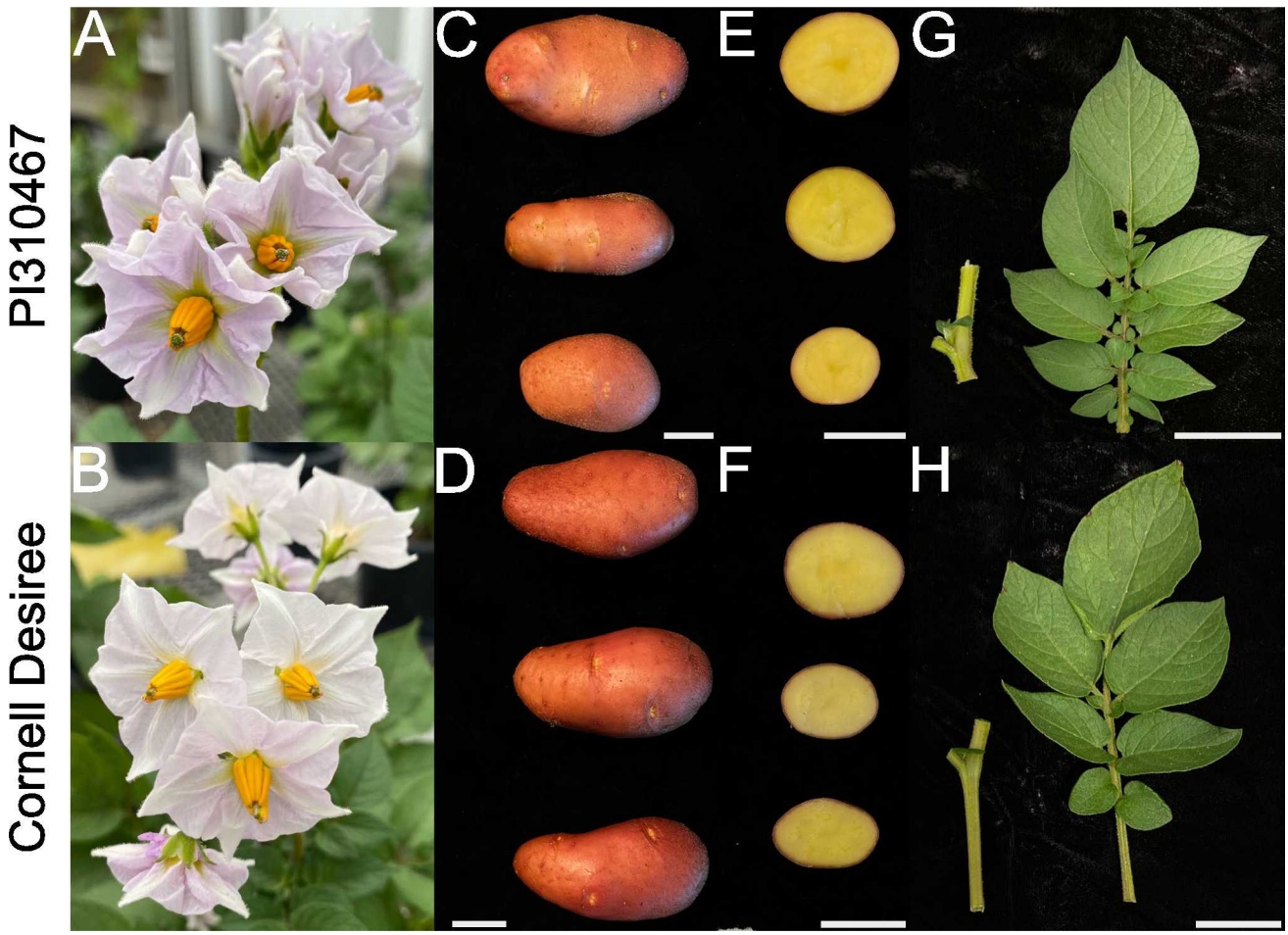

Fig. 1 Representative photographs of USPG Desiree and Cornell Desiree. Whole plant view from top from top (a–b), flowers (c–d), tubers (e–f) and tuber cross-sections (g–h). Bars: 2.54 cm (1 in)

also acquired from the USPG (USPG Urgenta hereafter) and subjected to whole genome sequencing. Reads were aligned to the DM1-3 v6.1 reference genome (Pham et al. 2020) and read depth was used to identify the chromosome 7 and 8 CNVs associated with tr8-7. Both the USPG and PTF Desiree holdings showed CNVs associated with tr8-7, but the other three Desiree holdings and USPG Urgenta did not (Fig. 2). To test whether tr8-7 was fixed within the USPG lineage, we skim sequenced three independent USPG Desiree cuttings acquired in 2019. Chromosome dosage analysis demonstrated that each cutting also carried tr8-7 (Supplemental Fig. S1), indicating that tr8-7 was fixed among the USPG Desiree holding. These data suggested that tr8-7 is polymorphic among Desiree holdings.

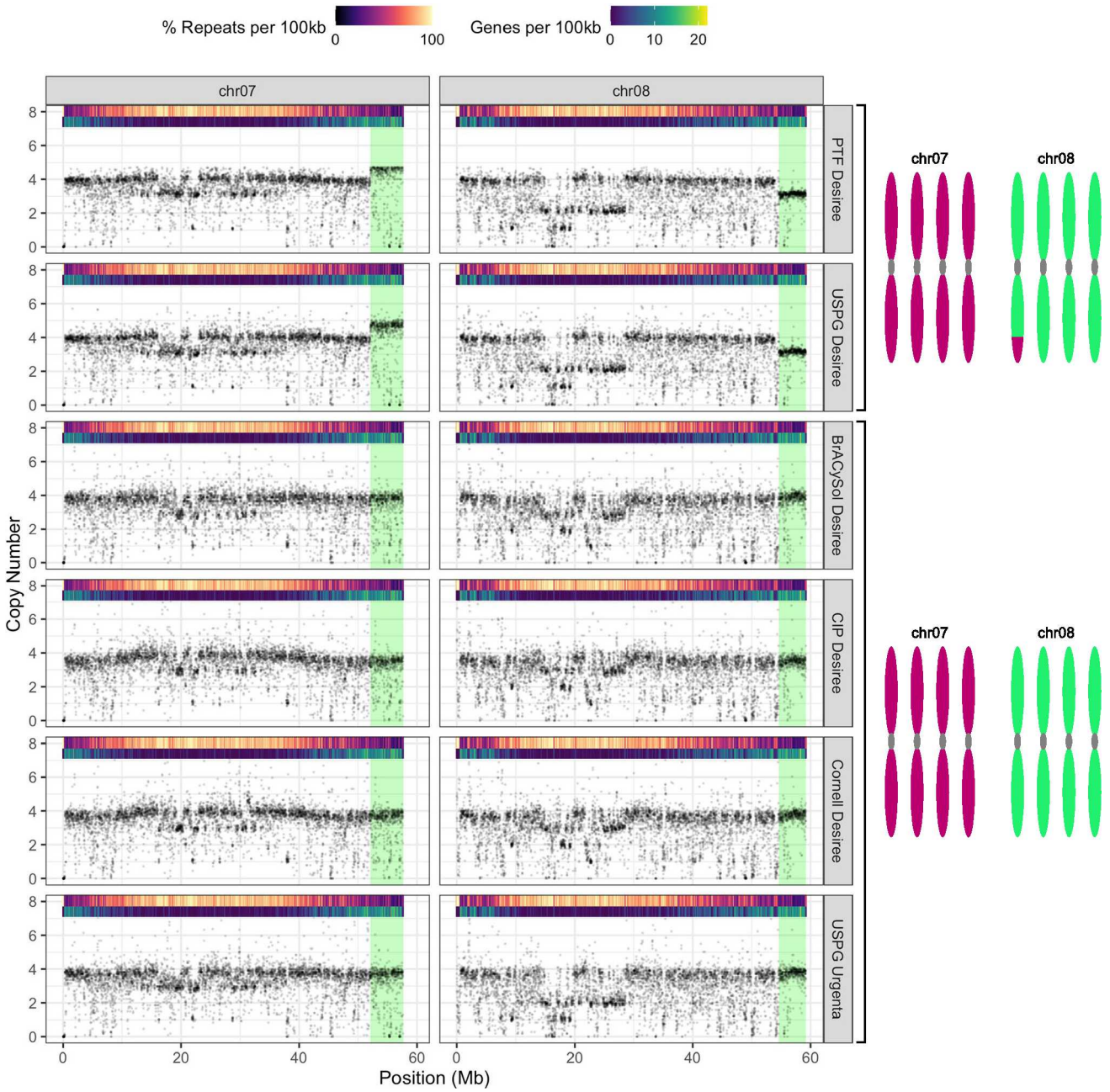

Fig. 2 Variation for the presence of the tr8-7 translocation among holdings of Desiree and Urgenta. Each panel represents a single accession and displays the median sequencing read coverage in non-overlapping 10 kb regions of chromosome 7 and 8. Tr8-7 is present in accessions that display 5 copies of the right end of chromosome 7 and three copies of the right end of chromosome 8. The green highlighting displays the regions affected by tr8-7. Points are plotted at high transparency

Translocation tr8 7 Arose Somatically

To determine how tr8-7 arose, we consolidated genotype information from tetraploid potatoes with publicly available SNP array genotypes (Hirsch et al. 2013; Endelman et al. 2017; Sharma et al. 2018; Prodhomme et al. 2020) and whole genome sequencing data. Our aims were to determine whether all Desiree and Urgenta holdings were true-to-type clones, and if not, to identify a match to the divergent clones from as diverse of a panel as possible. After consolidating these datasets, the final panel included genotype information for 1,181 samples at 1,640 SNPs, with good representation across all 12 chromosomes (Supplemental Fig. S2, Supplemental Table S1). To validate the data consolidation step, a neighbor joining tree was constructed using 96 clones that were genotyped across multiple studies but were not used for merging the datasets. Members of most duplicate groups exhibited short genetic distances (Supplemental Fig. S3), indicating that the dataset was merged correctly. Four duplicates were more distant from each other, suggesting other potential cases of mislabeled clones.

Seven Desiree holdings and two Urgenta holdings were represented in the panel. These holdings formed 3 clusters of nearly identical clones. The first cluster contained the Desiree holdings from BrACySol, CIP, Cornell and another two holdings from published SNP array data (Sharma et al. 2018; Prodhomme et al. 2020). The second cluster contained only the array-genotyped Urgenta holding from (Prodhomme et al. 2020) (Fig. 3), which did not match any other variety among the panel. These results indicate that at least some Urgenta and Desiree holdings were labeled incorrectly. By analysis of wild species introgressions, (Vos et al. 2015) concluded that their Urgenta holding, which was the same as Prodhomme et al. (2020) described, was incorrectly labeled. The third cluster contained Desiree holdings from the PTF and USPG as well as the USPG holding of Urgenta. Importantly, USPG holdings of Urgenta and Desiree were polymorphic for tr8-7 yet nearly identical by SNPs, indicating that tr8-7 was a somatic mutation.

The USPG Desiree Holding is a Mutant of Urgenta

To investigate which of the Desiree and Urgenta holdings were mislabeled, we inspected parent–offspring trios. For each trio, we report pedigree conflict, calculated as the percentage of monomorphic markers in both parents at which

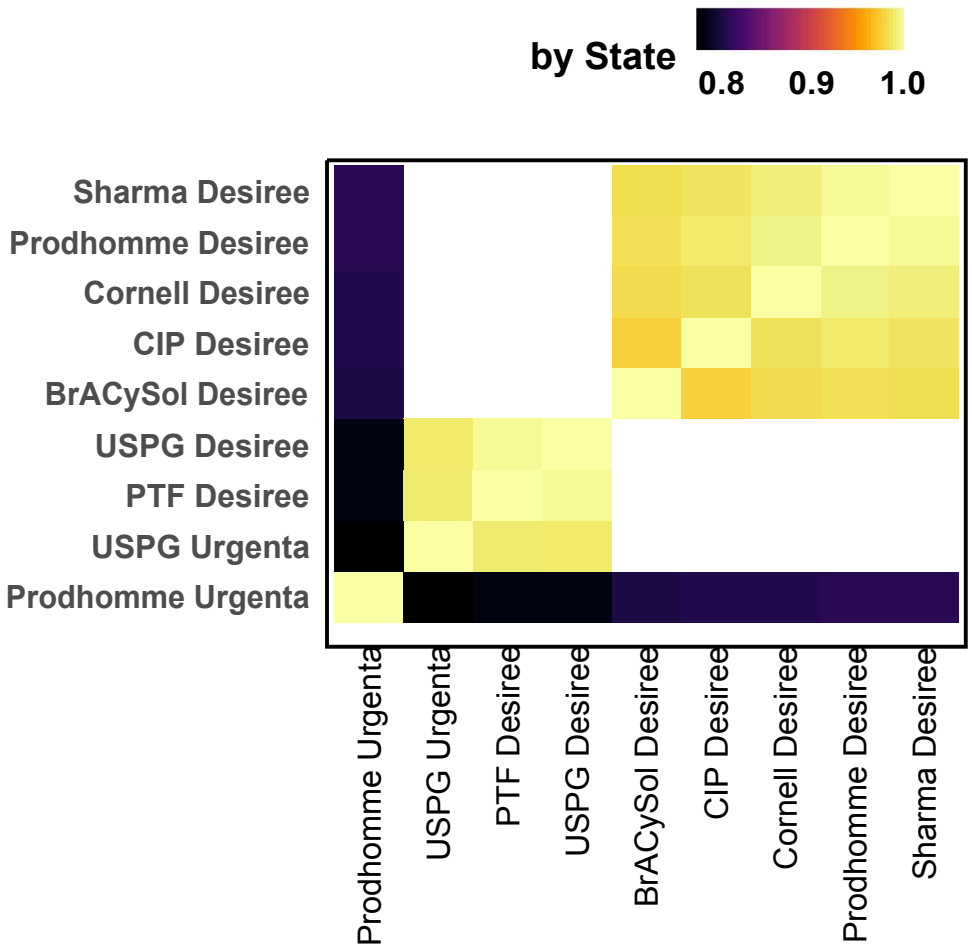

Fig. 3 Relationship between holdings related to or presumed to be Desiree. The heatmap illustrates pairwise identity by state between holdings of Desiree and Urgenta based on 1,642 genome-wide SNPs

the genotype of the offspring differed. For example, at a marker where both parents had a genotype of 0, a progeny genotype of anything other than 0 indicates a conflict. To first obtain an overview of the distribution for concordant and discordant trios, we calculated pedigree conflicts of 469 available trios. Conflict percentages fell into two clear categories: one consisting of 405 trios with conflict near 0% (range 0–4.15%), and 64 trios with conflict ranging between 12.6–57.0% (Supplemental Fig. S4). We concluded that pedigree information was correct for the 405 trios with conflict percentages near zero and incorrect for the other 64 trios (Supplement al Table S2). Even with fewer markers, we resolved known pedigree errors among North American germplasm (Endelman et al. 2017). We also identified eight new discordances from samples in the Sharma and Prodhomme panels (Supplemental Table S3).

Next, we inspected parent–offspring trios involving Desiree. As the identity of Urgenta was in question (Fig. 3) and genotypes of the paternal parent, Depesche, were not available, trio analyses with Desiree as offspring were not possible. However, there were five trios for which Desiree was a parent and each member of the trio was genotyped. When either the USPG or PTF Desiree holdings were presumed as parent, pedigree conflict was 14.49–31.32% for each of the five trios, indicating that they were not Desiree (Table 1). When Desiree holdings from BrACySol, CIP, Cornell or either SNP array dataset were assumed to be the parent, pedigree conflicts was close to 0% for three trios, and 14.1–16.3% for the remaining two trios (Table 1). We concluded that the Desiree holdings from BrACySol, CIP Cornell and both array datasets, but not from PTF or USPG, were true-to-type Desiree, and that the discordant trios with these holdings were due to pedigree errors.

We then tested trios involving Urgenta, a selection of Furore x Katahdin (van Berloo et al. 2007). Katahdin was represented three times in the panel. Furore was not genotyped, but it is the offspring of Alpha x Rode Star, which were both represented in the panel. As a stand-in for Furore,

Table 1 Trio conflict percentages of Desiree holdings

Offspring	Non-Desiree parent	Desiree parent	Tested Markers	Pedigree Conflict %
Stemster	Maris Piper	Sharma	230	0
		Prodhomme	230	0
		Cornell	230	0
		CIP	232	0.86
		BrACySol	231	0
		PTF	265	27.55
		USPG	265	27.55
Anya	Pink Fir Apple	Sharma	266	0
		Prodhomme	266	0
		Cornell	266	0
		CIP	267	0.37
		BrACySol	267	0.37
		PTF	274	17.88
		USPG	275	18.18
Saxon	Kingston	Sharma	219	21.00
		Prodhomme	219	21.00
		Cornell	219	21.00
		CIP	220	21.36
		BrACySol	219	21.00
		PTF	214	14.49
		USPG	214	14.49
Romano	Draga	Sharma	162	17.28
		Prodhomme	162	17.28
		Cornell	162	17.28
		CIP	162	17.28
		BrACySol	162	17.28
		PTF	182	31.32
		USPG	182	31.32

*Tested markers included only those that were homozygous for the same allele in both parents.

we used 370 SNPs that were monomorphic in Alpha, Rode Star and Katahdin for trio analyses with each of the candidate Urgenta holdings as offspring. The pedigree conflict was 0% when USPG holdings of either Urgenta or Desiree were used as offspring (Table 2). When the Urgenta holding from (Prodhomme et al. 2020) was used as offspring, the pedigree conflict was 47.44% (Table 2), supporting that this holding was erroneously named Urgenta, as (Vos et al. 2015) previously concluded. This result indicates that USPG Desiree is not Desiree, but a mislabeled Urgenta clone that carries tr8-7 as a somatic mutation.

To rapidly identify tr8-7, we developed PCR markers to amplify the tr8-7 junction. An 806 bp sequence flanking the tr8-7 junction was amplified from USPG and PTF Desiree holdings, but not from USPG Urgenta (Fig. 4a). Sanger sequencing of the PCR product did not reveal SNPs indicative of multiple haplotypes (Supplemental Fig. S5), suggesting that a single amplifiable DNA segment was associated with tr8-7. Alignment of the PCR product to the DM1-3 v6.1 reference genome revealed high-scor ing pairs (HSPs) near junction breakpoints on chromosomes 7 and 8 identified in a previous study (Comai et al. 2021). These HSPs flanked a 148 bp region that aligned to the consensus sequence of potato SINE family SolS-IIIa (Seibt et al. 2016) (Fig. 4a). These results indicate selective amplification of the tr8-7 junction.

Finally, to enable rapid identification of potentially mislabeled Desiree holdings, we developed and validated five CAPS markers that distinguished true-to-type Desiree from true-to-type Urgenta. From genome wide SNPs of Urgenta and Desiree holdings, we selected five BamHI CAPS markers on chromosomes 1, 2, 3, 4 and 6 for validation. Due to limited availability of genomic DNA, we genotyped only Cornell Desiree, PTF Desiree, USPG Desiree and USPG Urgenta. For all five markers, genotypes of each tested clone agreed with the predictions from genome sequencing (Fig. 4b, Supplemental Table S5, Supplemental Fig. S6). Together, the CAPS markers and junction PCR can be used to rapidly and inexpensively distinguish Desiree and Urgenta.

Table 2 Trio conflict percentages of Urgenta holdings

Parent 1	Parent 2	Offspring	Tested Markers*	Pedigree Conflict %
(Alpha x Rode Star)	Katahdin	Prodhomme Urgenta	137	47.44
		USPG Urgenta	137	0
		USPG Desiree	137	0
		PTF Desiree	137	0

*Tested markers included only those that were homozygous for the same allele in both parents.

Discussion

Clonal propagation enables somatic mutations to accumulate in independent lineages over time. Previously, we noticed that one Desiree holding carried translocation tr8-7, but other holdings did not, prompting us to investigate when and how the translocation arose. To address these questions, we compared the genomes of five Desiree clones from different institutions. Two of the five holdings carried tr8-7. SNP fingerprinting revealed that these holdings were clones, and trio analyses revealed that they were both Urgenta rather than Desiree. Urgenta is one of the two Desiree parents. An independent Urgenta clone validated by trio analysis did not exhibit tr8-7, indicating that tr8-7 arose somatically, possibly due to recombination between dispersed repeats. Other Desiree holdings from Cornell University, the International Potato Center, as well as laboratories and gene banks throughout Europe were confirmed as Desiree by trio analyses.

USPG Desiree was Urgenta^{tr8-7} by the time it was acquired by the UC Davis Plant Transformation Facility. Therefore, programs that received Desiree from this transformation facility or from USPG any time after approximately 1997, and perhaps earlier, can expect to have Urgenta^{tr8-7} instead of Desiree. Plant inventory records provide possible clues about the mixup. Tubers of Desiree and Urgenta were received on January 10, 1966 and designated PI310467 and PI310468, respectively, while the USPG Urgenta holding characterized in this study (PI21756 0) was imported May 1954 (United States Department of Agriculture 1960, 1969) (Fig. 5). Both cultivars make tubers with red skin and yellow flesh that may have been difficult to distinguish by eye. Characterization of PI310468 may provide additional insight, but unfortunately, it is no longer available from the USPG. The Urgenta clone with tr8-7 has been used for several studies in our laboratory at UC Davis. It can be readily regenerated from protoplasts (Fossi et al. 2019). To distinguish it from regular Urgenta or Desiree, we have named it Red Polenta.

Parent–offspring trio analyses using publicly available genotype and pedigree information were critical for identifying Red Polenta as a mislabeled Urgenta clone and tr8-7 as a somatic mutation. Similar exclusion analysis have resolved similar pedigree errors in potato (Endelman et al. 2017; Pandey et al. 2021). Even with fewer homozygous markers imposed by our use of genotypes across multiple studies, we validated known pedigree errors of North American cultivars (Endelman et al. 2017) and resolved pedigree errors of European cultivars. To enable ongoing validation of varieties and pedigree records, we encourage researchers to release genotype information in a

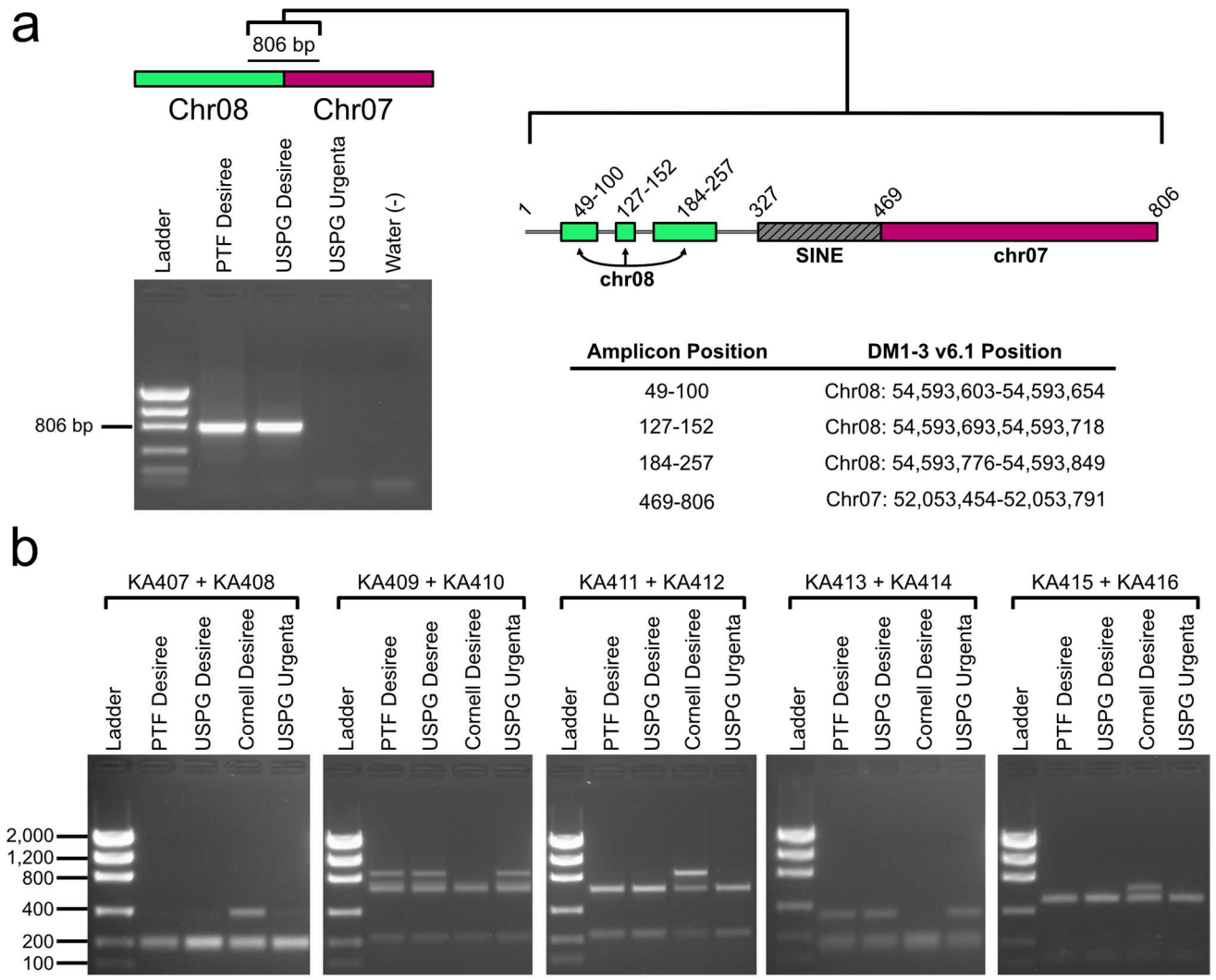

Fig. 4 PCR markers that distinguish Desiree holdings. a) tr8-7 junction amplification from PTF Desiree and USPG Desiree but not USPG Urgenta. Sanger sequencing of the PCR product and BLAST alignment to the DM1-3 v6.1 reference genome revealed high-scoring pairs, which are shaded according to the DM1-3 chromosome they were aligned to. Red: chr07. Green: chr08. b) Validation of Desiree-Urgenta CAPS markers. For each of five tested markers, PTF, USPG and Cornell Desiree holdings and the USPG Urgenta holding were genotyped. Expected product sizes of each marker are provided in Supplemental Table S5. Uncut controls for PCR product size and water-only controls for PCR amplification are shown in Supplemental Fig. S6

standardized format that facilitates reuse. Raw theta values (Schmitz Carley et al. 2017), or alternatively, allele dosage calls based on the DM1-3 reference genome and inclusion of other commonly genotyped varieties would be suitable. A good example is the genotype data from (Hirsch et al. 2013), which has been reused in at least eight studies (Hardigan et al. 2015; Kolech et al. 2016; Rosyara et al. 2016; Endelman et al. 2017; Schmitz Carley et al. 2017; Bastien et al. 2018; Garreta et al. 2021; Pandey et al. 2021).

By resampling independent lineages of Urgenta, we demonstrated the somatic origin of translocation tr8-7. Potato genomes are rife with structural variation, thought to be the combined effect of introgression from wild relatives and inability to purge somatic mutations accumulated during extended vegetative propagation (Hardigan et al. 2016, 2017; Zhou et al. 2020; Bao et al. 2022; Hoopes et al. 2022; Tang et al. 2022). Somatic mutations associated with obvious and even desirable phenotypes have contributed valuable bud sports in potato and many other crops (Foster and Aranzana 2018). We do not know the phenotypic impact of tr8-7. At the tetraploid level, genetic redundancy and buffering from gene dosage imbalance (Comai 2005) may decrease its impact. Field evaluation would be required to determine if the translocation has deleterious effects. Further, tr8-7 and other translocations transmitted through the germline yield primary dihaploids with segmental trisomy and/or monosomy (Comai et al. 2021). These aneuploidies could

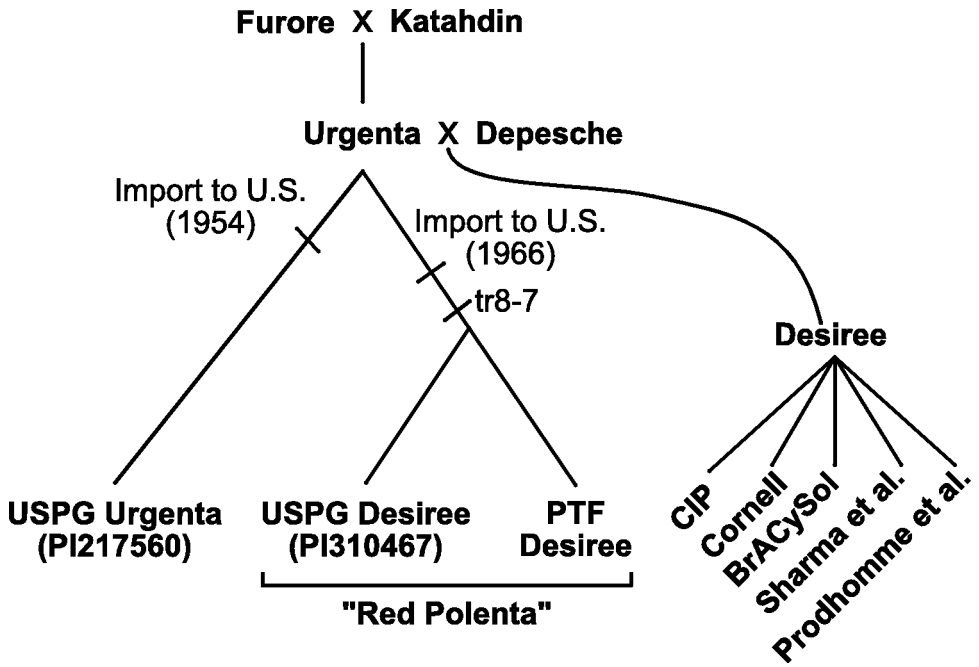

Fig. 5 Model for history of Urgenta and Desiree holdings throughout the context of their propagation and distribution. Urgenta, a selection of Furore x Katahdin, was delivered to the USPG twice: once in 1954 and again in 1966. The 1954 lineage gave rise to the current USPG Urgenta (PI217560). Both samples from the 1966 lineage carried tr8-7, indicating that the translocation arose prior to the divergence of current holdings of PTF Desiree and USPG Desiree (PI310467). Whether the translocation occurred before or after import is unknown. Urgenta was crossed with Depesche to give rise to Desiree, which was released in 1962. Current Desiree holdings from CIP, Cornell, BrACySol and the studies of Prodhomme et al. (2020) (via Vos et al. 2015) and Sharma et al. (2018) were true to type Desiree

hinder breeding efforts. As translocations could affect any breeding material, a simple solution to avoid their perturbing effect may be to characterize the genome of a tetraploid clone of interest before proceeding with outcrossing and/or dihaploid extraction, and if undesirable chromosome rearrangements are found, to characterize another institution's holding of the same cultivar.

In conclusion, we compared the genomes of multiple accessions of two cultivars, Urgenta and Desiree. Pedigree analysis validated the identity of holdings and revealed that the Desiree holding from the United States Potato Genebank is an Urgenta somatic variant carrying tr8-7, now called Red Polenta.

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Declarations

Conflict of Interests The authors declare that they have no conflict of interest.

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