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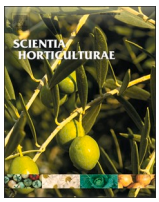

Genetic diversity in gooseberry (*Ribes uva-crispa*), as estimated with SSR markers

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ABSTRACT

European gooseberry (*Ribes uva-crispa* L.*)* is a popular berry crop in many European countries, including Sweden, Denmark and Ukraine. There is no active gooseberry breeding programme in either Sweden or Denmark, but a successful programme is operating in Ukraine. In Sweden and Denmark, research on gooseberries is primarily focused on collection and phenotypic evaluation of genetic resources. As part of these activities, a large number of inventory finds have been collected but have not yet been characterised morphologically or molecularly. The goal of this study was thus to characterise gooseberry germplasm with 15 simple sequence repeat (SSR) markers. From 242 accessions analysed, 153 unique genotypes were identified. Cultivars that have been in widespread cultivation in Sweden, such as the Finnish cultivars 'Hinnonmäen Keltainen' and 'Hinnonmäen Punainen', had relatively large numbers of synonymous samples. While many inventory finds were identifiable as synonyms of known cultivars, several were found to constitute unique genotypes within the germplasm studied. The studied genotypes clustered relatively well in three posterior groups, consisting of cultivars originating before and after the American gooseberry mildew (*Sphaerotheca mors-uvae*) outbreak around 1900 and cultivars originating from the territory of the former Soviet Union. A fourth genetic cluster consisting mainly of inventory finds from central and northern Sweden was also identified. In addition, it was possible to verify recorded and stipulated parentages for some of the cultivars studied and to identify three likely parent-parent-child trios. Thus, inventories of local gooseberry germplasm and a subsequent genotyping proved successful in finding unique local genotypes, with potential local adaptation. The data obtained provide a foundation for future studies of gooseberry genetic resources, while also illustrating the importance of a well-curated and phenotypically characterised set of reference cultivars for future studies.

1. Introduction

European gooseberry (*Ribes uva-crispa* L.) belongs to the genus *Ribes*, family *Grossulariaceae*, together with two other species of commercial interest, blackcurrant (*R. nigrum* L.) and redcurrant (*R. rubrum* L.). European gooseberry is a perennial vegetatively propagated small bush, normally 1.0 to 1.8 m in height and 1.0 to 1.2 m in width, often with spines on the branches and small leaves. The flowers are greenish or greenish with a pink tint, borne singly or in small clusters. The berries are round-oval, hairy or smooth, with size varying from approximately 1.0 to 2.5 cm in diameter and weight from 1.5 to 12 g. The berries vary in colour from white to yellow, green, red or dark red (Pluta, 2018).

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Gooseberry is native to large parts of central Europe, the Caucasus and North Africa (Welander, 1988). In addition to the native European gooseberry, there are several American species (for example *R. hirtellum* Michx.) that have been used in commercial breeding, mainly as a source of disease resistance to e.g. American gooseberry mildew (*Sphaerotheca mors-uvae* (Schwein.) Berk. & M.A.Curtis).

Gooseberry is a popular crop in many countries due to its attractive, tasty and nutritious berries with good storability (Vidyagina et al., 2021). Commercial gooseberry production is important in Austria, Czech Republic, Germany, Hungary, Poland, Russian Federation, Ukraine and the United Kingdom (UK) (Pluta, 2018). In other countries, gooseberries are produced only on a small scale. In Sweden, as in other Nordic countries, gooseberries are grown mainly in domestic gardens. In recent decades, breeding of new gooseberry cultivars has been conducted on a limited scale in Scotland and several countries in Eastern Europe, including Ukraine (Pluta, 2012). A breeding-orientated germplasm collection comprising 48 genotypes is available at the Institute of Horticulture, Kyiv, Ukraine.

There is currently no active gooseberry breeding programme in either Sweden or Denmark, but former breeding programmes have resulted in a number of cultivars. In Sweden, 'Scania', 'Centum' and 'Dr Törnmarck' were released in the 1930s and 'Jacob' in 1979 (Hjalmarsson and Wallace, 2007). The cultivar 'Tatjana' (synonym 'Uralski') was marketed in the 1990s in a Swedish-Russian cooperation. Today, research on gooseberries in Sweden is primarily focused on collection and preservation of genetic resources and gene bank-related work (Hjalmarsson, 2020; Hjalmarsson and Wallace, 2004). Similarly, Denmark has no active breeding programme and its research activities are focused on genetic resources.

In Sweden, conservation of heirloom cultivars of gooseberries is the responsibility of the *National Programme for Diversity of Cultivated Plants (Pom)*, which started its activities in 2000. As a result of its work, a Swedish National Gene Bank was established in 2016 to preserve so-called mandate cultivars. These are either cultivars developed locally or bred in Sweden, or foreign cultivars with a long growing tradition in Sweden (Hjalmarsson, 2020). Each mandate cultivar is kept in the gene bank fields at the Swedish University of Agricultural Sciences (SLU) in Alnarp. For security, additional backup collections are being established at the Swedish Elite Plant Station (EPS, Kristianstad, Sweden).

The original list of mandate cultivars, which was based on a literature review, consisted of about 30 cultivars and was finalised in conjunction with the launch of Pom's national inventory of fruit and berries in 2004. Unfortunately, only five of the 17 older Swedish cultivars on the list have been recovered and, due to their limited historical distribution and popularity, this number is unlikely to increase substantially in the future. In contrast, the majority of foreign mandate cultivars have been recovered and any remaining cultivars can most likely be retrieved from abroad. The original list of mandate cultivars was not intended to be permanent and has been amended over the years. Today, some 25 mandate cultivars (see Supplementary File 1) are kept in the National Gene Bank. However, the collection is likely to expand in the future as more cultivars are retrieved and inventory finds along with other interesting accessions are evaluated and added to the list.

Besides the mandate cultivars, it is known that much larger numbers of cultivars have been cultivated in Sweden in the past (Eneroth and Smirnoff, 1902; Pihl et al., 1887; Reimer, 1935). Thus, Pom's national inventory 2004–2010, which was directed towards the public, was aimed at locating additional old cultivars. It resulted in several finds being collected from private gardens, more or less all of which had no known cultivar name. Since 2018, a Swedish non-government organisation called Kålrotsakademien has also made efforts to recover historical cultivars (Ragnar et al., 2021). Materials have been gathered from commercial and institutional sources both within Sweden and abroad. Recently, Kålrotsakademien issued a call and conducted an inventory of cultivated gooseberry bushes maintained in household gardens.

Older gooseberry cultivars often lack detailed descriptions and thus it may be difficult to identify inventory finds and to verify that accessions kept in collections are correctly named. However, trueness-to-type is essential for material kept in gene banks, especially if it is made available for use in research and breeding. In addition, management of duplicates is costly. Therefore, in recent years molecular characterisation has become an important and accurate tool for verifying cultivar purity and ensuring trueness-to-type. It is also an effective method for uncovering duplicates within e.g. a collection of inventory finds and for estimating the genetic relationships between cultivars or accessions within a group of samples. Simple sequence repeat (SSR) markers have been frequently used for characterisation of germplasm collections of e.g. apple and pear (Denancé et al., 2020; Garkava-Gustavsson et al., 2013; Gasi et al., 2016; Larsen et al., 2017; Lassois et al., 2016; Sehic et al., 2012), and to some extent also for gooseberries and currants (Antonius et al., 2012; Droz et al., 2019; Karhu et al., 2012; Vidyagina et al., 2021).

In this study, 242 gooseberry samples from germplasm collections in Sweden, Denmark, UK and Ukraine were characterized with 15 SSR markers. Specific objectives were to: i) clarify the status of the gooseberry mandate cultivars preserved in the Swedish National Gene Bank; ii) characterise inventory finds and other germplasm collected from public and private gardens; and iii) evaluate the genetic diversity within Swedish gooseberry germplasm and compare it with that of cultivars preserved in Denmark and UK and germplasm used for breeding new cultivars in Ukraine.

2. Materials and methods

2.1. Plant materials

A total of 242 gooseberry samples were analysed in this study. Leaf tissue from cultivars preserved in Sweden (Swedish National Gene Bank, SLU Balsgård, and EPS), Denmark (Pometet, University of Copenhagen), and the UK (Chris Bowers & Sons and RHS) was collected, along with material from accessions used for breeding in Ukraine (germplasm collection at the Institute of Horticulture, Kyiv) and inventory finds collected in Sweden through Pom and Kålrotsakademien.

Branches from accessions in the Swedish National Gene Bank, at SLU Balsgård, at EPS, and Pom's inventory collection were collected in March 2021 and placed in a 200:1 mixture of water and a liquid fertiliser (Chrystal White). To initiate budburst, the branches were covered with plastic. Newly expanded leaf material was collected and placed in tubes for lyophilisation. The leaf material from Pometet was collected in October 2021 and lyophilised. The material originating from RHS, Chris Bowers & Sons and the Kålrotsakademien inventory was collected in Eppendorf tubes filled with silica gel and subsequently lyophilized after shipping. The material originating from the Institute of Horticulture, Kyiv, was collected in June 2021 and the DNA was immediately extracted from fresh leaves, air-dried and shipped to Sweden. The lyophilised material was stored at −80 °C.

All accessions studied are listed in Table 1 in Supplementary File 1. In the remainder of this manuscript, unique genotypes are noted by their preferred name and GooseBerry identifier as given in Table 2 in Supplementary File 1. Data on the age and origin of cultivars were taken primarily from Niggli and Frei (2019) and Eneroth and Smirnoff (1902), but occasionally from various other sources (Hedrick, 1925; Hogg, 1884; Reimer, 1935). Whenever recorded or hypothesised parentages of a cultivar were available from the above literature, the SSR profiles of the genotypes concerned were investigated for Mendelian errors. To account for the possibility of genotyping errors up to one mismatch was allowed, and relationships that were not in conflict with the SSR genotypes were noted as possible parents of a cultivar (Table 2 in Supplementary File 1).

Table 1
Locus name of the 15 simple sequence repeat (SSR) loci used in this study, size range of PCR product, sequence of forward and reverse primers, multiplex group, fluorescent dye, annealing temperature, number of alleles (Na), observed heterozygosity (H_o), expected heterozygosity (H_e) and fixation index (F).

Locus	Size range	Forward sequence	Reverse sequence	Multip. Grp.	Fluores. dye	Anneal. Temp.	Na	Ho	He	F
e1-O01	131–160	CCTTTCCAGAGAAAACTCAAACA	AAGTATGGGAACAACGGCAG	1	6FAM	60	7	0.66	0.56	−0.18
e1-O21	290–318	TCTCTCCAACTGAGAAGGAAAA	GATTTGTTCTTGTGCAGCGA	2	6FAM	54	11	0.15	0.16	0.03
e4-D03	160–238	CCCAAAAGCAAATTTAGGGT	GTGAGGCATGGAACCACTTT	1	PET	58	9	0.34	0.32	−0.07
g1-A01	205–254	CGAAGGTTGAATCGGTGAGT	CGTAGCCACGTAGTTCCACA	4	HEX	60	14	0.79	0.76	−0.04
g1-K04	277–298	TGTTCCCTGTTTCCTTCAAAA	GGACGTGGACGATGAGAGTT	3	6FAM	58	10	0.90	0.72	−0.25
g1-M07	199–232	TCCGTTACTGGAGTGGTGT	CCATGGTTTTCCGATTTGTT	4	PET	48	15	0.76	0.71	−0.06
g2-B20	139–191	CTCCATCAAATCCCTCGTTT	TCTTGCTTCCCAAACAGTATCA	2	PET	54	3	0.43	0.38	−0.14
g2-G12	164–194	GTGACCCACCTAAACCGTCC	GGAGTGGAGGGTTGGAAAAT	4	6FAM	62	2	0.18	0.16	−0.10
g2-H21	238–272	TGCCCTTTTTGGTCATTTTC	CAATCGTCGATGAAGGTCTG	1	HEX	54	11	0.55	0.54	−0.01
g2-J08	140–181	CGCCGAGCTCTAATCACTGT	ATAGCCCATGCCCATATTCA	3	NED	60	11	0.48	0.51	0.06
g2-L17	114–166	TTTGGAAAACCTCCCCTTT	GAGCTGTTGCTGTTGCCATA	2	HEX	56	19	0.64	0.62	−0.03
gr2-J05	160–186	CAAAACTGATTAGGGATCA	TTTGAAGAAGAGATGGCGAAA	3	HEX	54	8	0.59	0.62	0.05
MTT-5	144–244	GCGATTCCATTACGACACTTTGCA	ATAGGCAAGCATCACCTCACC	1	NED	52	30	0.84	0.88	0.05
RJL-7	200–238	TCCCGTTACTGGAGTGGTGT	CCATGGTTTTCCGATTTGTT	2	NED	50	16	0.78	0.73	−0.07
RJL-11	215+	CGAAGGTTGAATCGGTGAGT	TTGTGAGCCGTAACCACGTA	3	PET	56	14	0.78	0.77	−0.02
Mean	–	–	–		–	–	12	0.59	0.56	−0.05

2.2. DNA isolation

Genomic DNA of all samples except those from the Ukrainian collection was isolated either from around 20 mg of lyophilised leaf tissue or from 80–100 mg of fresh leaf material, using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. For Ukrainian samples, DNA extracted previously using the CTAB method with minor modifications (Doyle and Doyle, 1987) was obtained from the Institute of Horticulture, Kyiv. The quality and concentration of all DNA samples were assessed by Nanodrop (ThermoFisher Scientific Inc.) measurements. All DNA samples were also run on 1.5% agarose gel stained with GelRed® Nucleic Acid Gel Stain (Biotium, USA) and visualised under UV light to confirm that the DNA was not degraded.

2.3. SSR-analysis

The 15 SSR markers were chosen based on proven usefulness in detecting polymorphism and amplifying SSR loci in both gooseberry and currants in previous studies (Droz et al., 2019; Gunnarsson, 2009; Mezhnina and Urbanovich, 2017; Palmieri et al., 2013; Pikunova et al., 2015). PCR reactions were prepared according to the manufacturer's instructions and conducted in a 10 μl volume containing 5 μl Dream Taq PCR Master Mix (2X) (Thermo Scientific Baltics, Lithuania), 0.5 μM forward and 0.5 μM reverse primer, 3 μl milli-Q water, and 1 μl template DNA (20–40 ng). Amplifications were conducted with each primer-pair separately. The conditions were as follows: initial denaturation at 95 °C for 2 min, 25 (or 30 in case of g2-G12) cycles consisting of denaturation at 95 °C for 30 s, annealing at a primer specific temperature for 1 min, and elongation at 72 °C for 1 min followed by a final elongation step at 72 °C for 5 min. The annealing temperature for all the loci are presented in Table 1.

To ensure consistency in the results, five samples from the previous plate were run on a consecutive plate and compared with the previous run and the first five samples on each plate were repeated within the PCR plate.

PCR products were run on 1.5% agarose gel stained with ethidium bromide and visualised under UV light to verify the amplification quality. For capillary electrophoresis, PCR products were multiplexed in four groups based on allele size and fluorescent label and analysed on a 3500 Series Genetic analyzer (Thermo Scientific, USA). The fluorescent label used for each primer, their annealing temperature, and their multiplex groupings are listed in Table 1.

2.4. Data analysis

Alleles were called automatically in the GeneMarker 3.0.1 software (SoftGenetics LLC) and then curated manually. Allele frequencies (A), observed heterozygosity (H_o), expected heterozygosity (H_e), fixation index (F) and genetic distances were calculated in GenAlEx 6 (Peakall and Smouse, 2012). Accessions with identical or near-identical SSR profiles were identified and all accessions were assigned to one of the four classes previously proposed in the literature (de Andrés et al., 2007): Class 1, comprising accessions with unique SSR profiles; Class 2, comprising accessions with similar names and identical SSR-profiles; Class 3, comprising known synonyms or sports and similar SSR profile; or Class 4, comprising mislabelled samples. Class 4 is further subdivided into Class 4a, denoting accessions with similar names and different SSR profiles, and Class 4b, denoting accessions with different names but identical SSR profiles. Duplicate genotypes were visualised as network plots using the iGraph package (Csardi and Nepusz, 2006) in R (R Core Team, 2020). The average probability of identity (PI), i.e. the probability that two randomly selected samples have identical SSR profiles by chance, and more conservatively considering the possibility of a group of siblings (PI_sib) were calculated in GenAlex. To mitigate uncertainties in the naming of samples, each unique genotype was assigned a GooseBerry (GB) identifier (GB_1 to GB_153), to clarify the reference to certain SSR profiles.

Genetic structure was assessed using unique genotypes. Genetic distances were calculated in GenAlex and used for principal coordinate analysis (PCoA). Eight individuals that failed to produce bands for two of the loci were treated as being homozygous for null alleles, rather than as missing values. To visualise highly similar accessions not considered synonymous in the present study, an unweighted pair-group method using arithmetic averages (UPGMA) tree was generated from the genetic distance matrix using MEGA11 (Tamura et al., 2021), for ease of

comparison with future studies (Supplementary File 2). Genetic structure was analysed statistically by the model-based clustering approach implemented in STRUCTURE v2.3.4 (Falush et al., 2007, 2003; Pritchard et al., 2000), run with Parallel GNU (Tange, 2011). Five independent replicate runs were performed, assuming 1–10 subpopulations (K) with a burn-in of 15,000 and a run length of 100,000 for each K. Most probable number of subpopulations was determined using the Evanno method as implemented in Structure Harvester (Earl and vonHoldt, 2012; Evanno et al., 2005). Average individual assignment probabilities were calculated using CLUMPP v.1.1.2 (Jakobsson and Rosenberg, 2007) and graphical displays were generated using DISTRUCT v1.1 (Rosenberg, 2003). Genotypes were assigned to the subpopulation with which they had the highest membership coefficient if ≥ 0.8, while genotypes with a membership coefficient of < 0.8 to all subpopulations were designated 'admixed'. Prior groups were assigned based on cultivar origins, where: cultivars originating from before 1900 were assigned to the group 'Pre-1900', cultivars originating from after 1900 were assigned to the group 'Post-1900', cultivars from Ukrainian breeding germplasm were assigned to the group 'Ukr.', inventory finds were assigned to the group 'Invf.', and cultivars of unknown age were assigned to the group 'Other' (Supplementary File 2). The year 1900 was used as the threshold for prior group assignment as the American gooseberry mildew became widespread in Europe around that time. Prior group assignments were not used as prior information on location for STRUCTURE.

In eight cases, recorded or stipulated parentages were verified by absence of more than one Mendelian error in the SSR profiles of the parent-offspring pair. Additional possible parent-offspring relationships were identified using FRANz v.2.0.0 (Riester et al., 2009), which employs a Bayesian approach to pedigree reconstruction using maximum likelihood, accounting for multiple generations. Four runs were performed with different seeds and values for the maximum number of candidate fathers in the population (Nmax = 10, 50, 100, 200), otherwise using the default settings. For 69 accessions, data on approximate year of origin were available and were thus included in the model. The previously mentioned eight cases of verified parent-offspring relations were also included as prior information in the analysis. Only parent-parent-offspring assignments (trios) with posterior probabilities greater than 0.90 in all four runs, parent-pair log-odds ratio (LOD) scores above 10, and no mismatches were considered as likely parent-offspring relations.

3. Results

3.1. SSR-loci

The number of alleles varied from 2 (g2-G12) to 30 (MTT-5). Observed heterozygosity (H_o, 0.15–0.90) was close to the expected value (H_e, 0.16–0.88) for each locus. Fixation index (F) was close to zero or slightly negative (from −0.25 to −0.06), where a negative F value indicates an excess of heterozygotes that might be caused by negative assortative mating or balancing selection. Accordingly, *Ribes* species have been found to be at least partially self-sterile (Denisow, 2003; Offord et al., 1944), and are probably outcrossers like most long-lived perennials (Gaut et al., 2015).

Despite repeated attempts, eight accessions from the germplasm collection in Kyiv did not produce any PCR products for the g1-A01 locus. Two of these accessions also consistently failed to produce a PCR product for the g2-L17 locus. All other samples were successfully called for all loci. As this was observed in the breeding germplasm from Ukraine only and at specific loci, it might indicate a specific exotic contribution to their gene pool. In addition, two of these eight cultivars ('Karat' and 'Neslukhivski', GB_146 and GB_147) are full siblings according to the pedigree records. The average PI was lower than 0.001 already at five SSR loci, and the average PI_sib was lower than 0.001 for 12 SSR loci (File S1). This indicates that the 15 SSR loci used in this study are sufficient for reliable identification of synonymous samples.

3.2. Unique and duplicate accessions

From amongst the 242 accessions and inventory findings analysed, 153 unique genotypes were identified. These were classified into: 114 accessions with unique names and SSR profiles (class 1), six pairs of accessions with similar or identical names and identical SSR-profiles (class 2), seven cases of accessions sharing the same name, but not SSR profile, with other accessions (class 4a), and 27 groups of accessions with different names but with identical SSR profiles (class 4b). Very few genotypes were represented by more than two accessions. The three groups with the largest number of synonymous accessions were 'Hinnonmäen Keltainen' (11 samples, GB_32), 'Hinnonmäen Punainen' (10 samples, GB_78) and 'Bright Venus' (8 samples, GB_3). All accessions from the breeding germplasm from Kyiv had unique profiles, regardless of their non-amplifying loci. No cultivars were assigned to Class 3, since no known sports were analysed in this study (Fig. 1a, Supplementary File 1).

3.3. Genetic structure

The first two dimensions of the PCoA analysis explained 13.2 and 9.4% of the genetic variation, respectively. The prior group assignments resulted in considerable overlap between groups considering the first and second dimensions of the PCoA (Fig. 1b). The STRUCTURE analysis indicated that the collection could be separated into four subpopulations as ΔK peaked at $K = 4$, L(K) was higher for $K = 4$ than for lower numbers, and a meaningful proportion of the genotypes could be assigned to either of the four subpopulations. Based on their composition, these posterior clusters were denoted 'Old', 'Modern', 'Eastern', and 'Northern' (Fig. 1c, 1d, Supplementary File 1). The first three of these posterior clusters seemed to agree with the prior groups, with a majority of the genotypes assigned to the prior 'Pre-1900' group being assigned to the posterior 'Old' cluster. The known cultivars assigned to the posterior 'Modern' cluster were mostly from the prior 'Post-1900' group. All genotypes from the prior 'Ukr'. group clustered in the posterior 'Eastern group', together with most other cultivars with names indicating an origin in the region of the former Soviet Union and the Finnish cultivars 'Hinnonmäen Keltainen' (GB_32) and 'Hinnonmäen Punainen' (GB_78). Half of the genotypes assigned to the prior group 'Other', all with names indicating an origin within the territory of the former Soviet Union, were assigned to the 'Eastern' posterior cluster. An additional fourth cluster, the Northern cluster, identified by the STRUCTURE analysis had no prior counterpart. It comprised 11 inventory finds from central-northern Sweden clustered together with a local cultivar from northern Sweden, 'Ångermanlands Röda' (GB_64), and was designated as the 'Northern' cluster. Of the genotypes assigned to the prior group 'Invf.' that were not admixed, half were assigned to the 'Old' posterior cluster. The 'Modern' and 'Eastern' posterior clusters made up equal minor proportions of the 'Invf.' group. Introgression of mildew resistance according to literature was equally common in the 'Modern' and 'Eastern' clusters, and completely absent in the 'Old' and 'Northern' posterior clusters (Supplementary File 1). Overall, 23% of the unique genotypes were found to be admixed.

3.4. Pedigree analyses

Recorded or stipulated pedigrees were fully (both parents) or partially (one parent or one parent and one or two grandparents) verified for eight genotypes: 'Greenfinch' (GB_121), 'Grüne Kugel' (GB_122), 'Invicta' (GB_35), 'Jacob' (GB_36), 'Keen's Seedling' (GB_81), 'Landströms Gröna Seedling' (GB_41), 'Red Jacket' (GB_93), and 'Ronja' (GB_54). In some cases, genotypic data on both parents were available and could be confirmed, such as for 'Red Jacket' ('Houghton' x 'Red Warrington'), while in other cases only one parent could be confirmed,

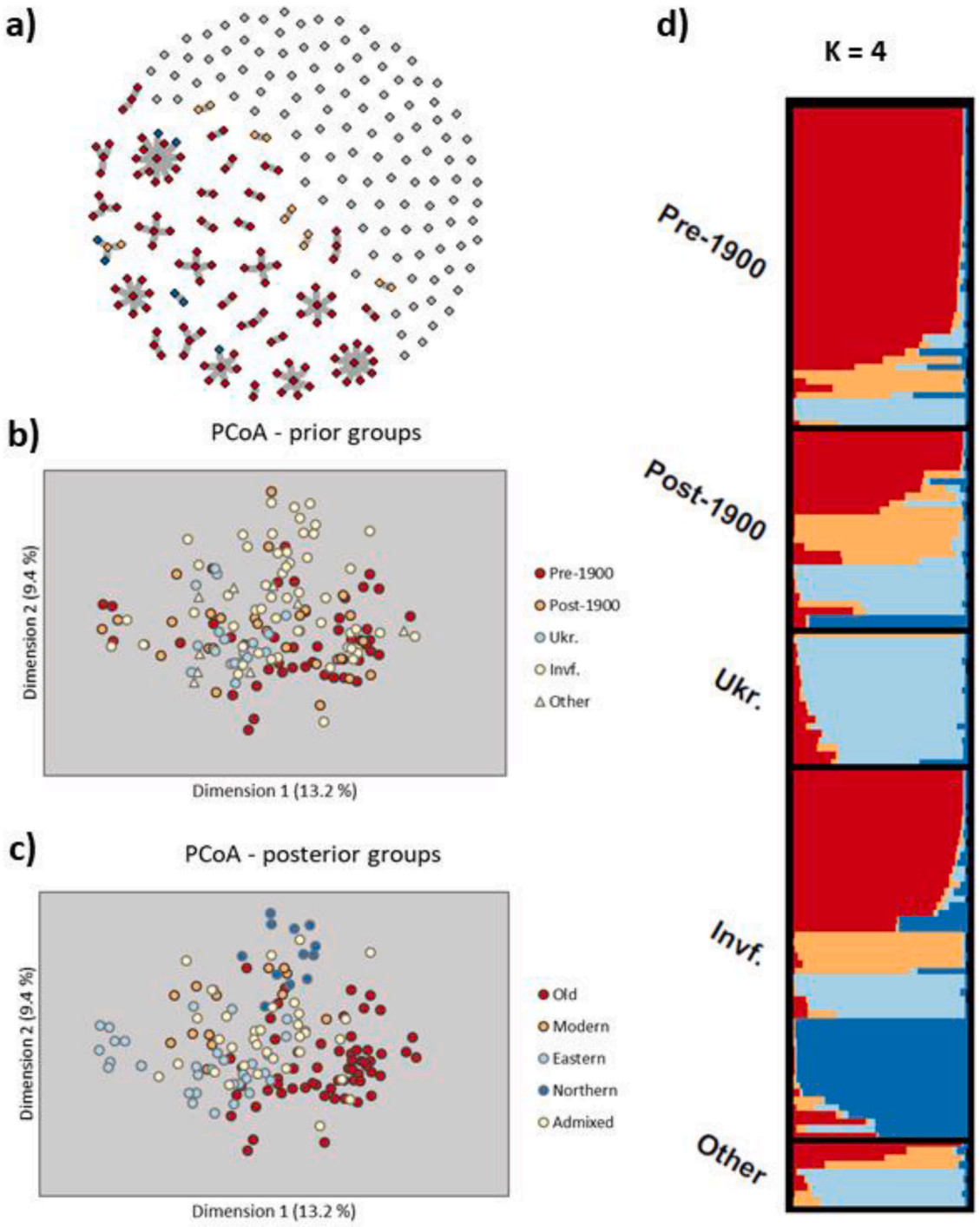

Fig. 1. Duplicate samples and genetic structure. a) Network plot illustrating the de Andrés classification, where Class 1 accessions are grey, Class 2 are beige, Class 4a are blue and Class 4b are red. Duplicate genotypes are connected by grey lines between beige and red dots. Blue dots are connected with lines to accessions sharing the same name. b) Unique samples plotted according to the first and second dimensions of PCoA and coloured according to the prior groups 'Pre-1900', 'Post-1900', 'Ukr.', 'Invf.' and 'Other'. c) Unique samples plotted according to the first and second dimensions of the PCoA and coloured according to the posterior groups 'Old', 'Modern', 'Eastern', 'Northern' and 'Admixed' based on STRUCTURE analysis. d) Graphical display of results of the proportion of ancestry for $K = 4$ groups, by prior group, where colours are the same as for (c). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

e.g. for 'Ronja' ('London' x 'Hinnonmäen Punainen') only the recorded ovule donor 'London' (GB_45) could be confirmed as a parent of 'Ronja' (GB_54).

There were also cases where genotypic data were available and could be confirmed for one parent and one or two grandparents, such as for 'Greenfinch' ('Careless' x ('Whinhams Industry' x 'Resistenta')) and 'Jacob' (('Whitesmith' x *R. oxycanthides*) x 'Achilles'). Notably, two non-synonymous accessions were named 'Achilles', both with SSR profiles matching the recorded pedigree for 'Jacob'. One of these (GB_24) was sampled at the Swedish breeding station in Balsgård, and since 'Jacob' is a Swedish cultivar we assigned this genotype the preferred name 'Achilles'. The other sample (GB_102) came from the Danish collection

Pometet, and was assigned the preferred name 'Achilles (Uncertain)'. However, these two shared one allele in each locus and thus one may have been a seedling from the other.

In some cases, the recorded pedigree could be confirmed, which helped identify incorrectly labelled accessions. This was the case for 'Invicta' ('Keepsake' x ['Resistenta' x 'Whinham's Industry']), where samples with different SSR profiles were initially labelled 'Keepsake'. As only one of the genotypes had an SSR profile matching a parent-child relationship with 'Invicta' (GB_35), that sample was assigned the preferred name 'Keepsake' (GB_82), and the other sample was assigned the preferred name of another sample with identical SSR profile, 'Careless' (GB_108).

It has been hypothesised that 'Keen's Seedling' (GB_81) might be a chance seedling of 'Red Warrington' (GB_97) (Eneroth and Smirnoff, 1902), which is in agreement with their SSR profiles. Similarly, based on propagation history and phenotype, sample number 65 (GB_41) was suspected to be a chance seedling of 'Landströms Gröna', which is in agreement with their SSR profiles, so GB_41 was denoted 'Landströms Gröna Seedling'.

In addition to these confirmed pedigrees, three likely trios in the collection were identified (Table 2). 'Ångermanlands Röda' (GB_64) was found to be a likely offspring of Inv_43 (GB_31) x Inv_2 / Inv_15 (GB_2). Inv_43 is an inventory finding from the same region in northern Sweden as 'Ångemanlands Röda', while the genotype GB_2 is represented by two inventory findings from the same garden in southern Sweden (Småland). 'Ångermanlands Röda' was found to be involved in another likely trio, this time as a parent of Inv_55 (GB_50) in the cross 'Champagne Yellow' (GB_71) x 'Ångermanlands Röda' (Table 2). The third trio identified, 'Resistenta' ('Robustenta' x 'Perle von Münchenberg'), consists of three cultivars that were bred by the same breeder and released in the same year (Keep, 1975; Niggli and Frei, 2019). Thus, it is highly probable that they are closely related, either as a trio or through some other close relationship.

4. Discussion

In this study, it proved possible to assign cultivar names to several inventory finds based on their SSR profile. For example, all unidentified accessions collected from the Sofiero castle garden (samples 89–93, Supplementary File 1) were identified as synonymous with known and widely grown old cultivars ('Alicant', 'Achilles', 'Aaron' and 'Whinham's Industry').

Accessions representing cultivars that have been extensively grown, such as 'Hinnonmäen Keltainen' (GB_32), were found to have an SSR profile identical to that of several other samples, indicating that these are duplicates of the commonly grown cultivar. Other cultivars which have been widely cultivated in Sweden, and accordingly had several synonymous inventory finds, were 'Aaron', 'Green Willow', 'Hönings Früheste' and 'Whinham's Industry' (GB_26, GB_44, GB_16, and GB_34, respectively). On the other hand, in some cases several inventory finds were found to be synonymous, indicating that they represent common cultivars, but no known cultivar samples were found representing that genotype so the identity remains unknown (e.g. GB_14 and GB_27). As illustrated above, the availability of recorded pedigrees also helped identify the correct name for a genotype in the case of several samples with the same name, but different SSR profiles, as was the case for 'Keepsake', 'Careless', 'Achilles', and 'London'.

Accessions assigned to Class 1 were consistently given the accession name as the preferred name in this study. It should be noted, however, that without morphological comparisons with pomological literature or available established reference accessions, such assignment of names to genotypes is only provisional. Several inventory finds had unique SSR profiles and might be either unique samples of unknown cultivars or chance seedlings. The relatively large proportion of unique inventory finds might indicate that gooseberry frequently produces seedlings. For example, the sample 'Landströms Gröna Seedling' (GB_41) was found as a branch with phenotype deviating from the rest of a bush of 'Landströms Gröna' (GB_40) in a clonal archive. It was thus hypothesised to be a chance seedling, which was confirmed by the SSR profiles of the samples. Similarly, the accession 'False Dr Törnmarck' (GB_29) was originally labelled 'Dr Törnmarck', but had a deviating phenotype. Thus it was hypothesised to be a seedling, although no sample likely to be true-to-type 'Dr Törnmarck' was available to confirm it as a parent of the putative seedling. Similarly, two inventory finds from the same garden (GB_ 42 and GB_60) had very similar SSR profiles, indicating that they might be sibling seedlings.

Further complications can be introduced if the same name is used for more than one cultivar or if accession names are misspelled. The cultivar 'Mountain' has traditionally been called *bergskrusbär* (Eng. *mountain gooseberry*) in Sweden, while the cultivar 'Houghton' has been marketed as *bergskrusbär* in Swedish-speaking parts of Finland. In Denmark 'Houghton' has traditionally been referred to as *bergstikkelbær* (Eng. *mountain gooseberry*). Thus 'Mountain' and 'Houghton' have the same common name in the Nordic countries, even though they represent unique separate genotypes clustering to different posterior groups (Supplementary File 1). Regarding misspelled cultivar names, the sample of 'Careless' (GB_108) and one of the accessions of 'Bedford Red' (GB_105) were originally registered as "Caraless" and "Bedford Reel", respectively. While these cases were easily identified, misspellings can accumulate over time, illustrating the advantage of unique numeric genotype identifiers as previously applied to apple and pear cultivars (Denancé et al., 2019; 2020).

The proportion of trios (1.9 trios per 100 unique genotypes) detected was slightly lower than in similar studies in apple using SSR markers (3.2 and 2.5 trios per 100 unique genotypes) (Lassois et al., 2016; Urrestarazu et al., 2016), which might be caused by smaller sample size or different evaluation criteria for accepting trios. If gooseberries are very prone to producing chance seedlings, it would also be less likely for the offspring and both parents to be retained in cultivation and preserved in the clonal archives. However, it should be noted that establishing a more extensive and reliable assessment of parent-offspring relationships would require a high-density marker system such as single nucleotide polymorphisms (SNP) arrays (Howard et al., 2021; Muranty et al., 2020; Skytte af Sätra et al., 2020), which is currently not available for gooseberry, or Genotyping by Sequencing (GBS) (Larsen et al., 2018).

5. Conclusions

Use of genetic markers can provide substantial aid in curation of gene bank material, as it enables reliable and relatively rapid identification of synonymous samples. This means that the number of accessions for which morphological characterisation is necessary can be greatly reduced, allowing more thorough examination of the remaining accessions. In this study, some of the most widely cultivated gooseberry cultivars in Sweden, such as 'Hinnonmäen Keltainen', were represented by multiple synonymous samples. However, a large number of inventory finds were found to be unique genotypes within the germplasm samples analysed. The genetic structure was found to be characterised by three anticipated groups: western European cultivars originating from before

Table 2
Trios identified in the study and their log-odds ratio (LOD) score. Parent1 and Parent2 do not indicate ovule and pollen donor, as these cannot be identified in the absence of cytoplasmic markers.

Offspring	Parent1	Parent2	LOD
'Ångermanlands Röda' (GB_64)	Inv_43 (GB_31)	Inv_2 / Inv_15 (GB_2)	24.0
'Resistenta' (GB_52)	'Robustenta' (GB_53)	'Perle von Münchenberg' (GB_49)	27.5
Inv_55 (GB_50)	'Champagne Yellow' (GB_71)	'Ångermanlands Röda' (GB_64)	18.0

and after the American gooseberry mildew outbreak around year 1900, and cultivars originating in the territory of the former Soviet Union. A fourth cluster consisting mainly of inventory finds from central and northern Sweden was also identified. Thus, gooseberry inventories seem to be successful at finding unique accessions that are most likely seedlings with the potential to spread further as locally adapted cultivars. The large number of unique inventory finds also highlights the importance of access to a large set of morphologically well-characterised accessions with documented origin for comparison in future studies.

CRediT authorship contribution statement

Josefine Nordlander: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Jonas Skytte af Sätra:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Funding acquisition. **Helena Mattisson:** Methodology, Writing – review & editing, Supervision. **Kateryna Udovychenko:** Validation, Investigation, Resources, Writing – review & editing. **Olga Lushpigan:** Resources, Writing – review & editing. **Lasse Lose:** Resources, Writing – review & editing. **Hans Naess:** Resources, Writing – review & editing. **Matti Leino:** Methodology, Validation, Formal analysis, Investigation, Resources, Writing – review & editing. **Inger Hjalmarsson:** Conceptualization, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing, Funding acquisition. **Larisa Garkava-Gustavsson:** Conceptualization, Methodology, Validation, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2022.111438.

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