Redundancies and Genetic Structure among ex situ Apple Collections in Norway Examined with Microsatellite Markers

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Abstract. Apple genetic resources in Norway are currently conserved within a number of local clonal archives. However, during establishment of these ex situ collections, primary focus was not on capturing as much of the diversity as possible, but instead on preserving cultivars of particular importance to specific fruit-growing areas. To identify redundancies within the collection as well as to assess the genetic diversity and structure of apple germplasm currently being conserved in Norway, eight microsatellites were used in genetic characterization of 181 apple accessions. Overall, 14 cases of synonym or possibly mislabeled accessions were identified, as well as several homonyms and duplicates within and among the analyzed collections. The information obtained should contribute to overall better management of the preserved germplasm. Bayesian analysis of genetic structure revealed two major clusters, one containing most of the foreign cultivars, while the other consisted mainly of traditional Scandinavian cultivars, but also some very winter-hardy genotypes such as ‘Charlamovsky’, ‘Gravenstein’, ‘Transparente Blanche’, and ‘Wealthy’. Analyses of molecular variance (AMOVA) detected a significant genetic differentiation among the clusters ($f_{CT} = 0.077$; $P < 0.01$). The results of the Bayesian analyses do not indicate a strong differentiation between the foreign and the Norwegian apple accessions, however, they do suggest that climate adaptation has had a significant influence on the genetic structure of the preserved germplasm. Overall, apple accessions currently maintained ex situ in Norway represent a diverse germplasm which could be very valuable in future breeding programs, especially for the Scandinavian climate.

Modernization of fruit production in Norway in the last few decades has led to the clearing of old orchards, containing traditional cultivars, to make room for high-density orchards, planted with modern international cultivars. In order not to lose the traditional fruit germplasm permanently, collecting missions focusing mainly on apple were initiated in the 1980s and 1990s

(Hjeltnes, 2008). The overall focus of this undertaking was not primarily concerned with capturing as much of the Norwegian fruit genetic diversity as possible, but instead traditional cultivars of particular importance to specific fruit growing areas were collected and conserved within a number of local clonal archives.

Since the collecting efforts were decentralized and mainly conducted by enthusiastic volunteers, methodology and selection criteria for which genotypes should be conserved in the local clonal archives, varied greatly. Consequently, the presence of misidentified accession, among the collections, is probably rather high. Although passport data have been collected for most of the accessions, to efficiently manage the conserved apple germplasm in Norway, a more detailed and objective characterization is needed. DNA markers are much more efficient, compared with traditional morphological

(e.g., pomological) characterizations, in revealing mislabeled plant accession (Nyblom and Weising, 2010). Microsatellite markers, also known as simple sequence repeats (SSRs), have shown great promise as a tool for managing *Malus* ex situ germplasm collections as well as for collection and preservation strategies of these genetic resources (Hokansson et al., 1998). Characterizing accessions maintained in ex situ apple collections, using microsatellite markers, has so far been performed in a number of countries such as Sweden, Finland, Bosnia and Herzegovina, Italy, United States, France, Spain, Holland, and most recently on a Pan-European level (Garkava-Gustavsson et al., 2008, 2013; Gasi et al., 2010, 2013b; Hokanson et al., 2001; Lassois et al., 2016; Liang et al., 2015; Pereira-Lorenzo et al., 2007; Urrestarazu et al., 2012; van Treuren et al., 2010; Urrestarazu et al., 2016). Although the number of examined apple accessions and used SSRs has varied greatly among the mentioned studies, the obtained results have helped increase the efficiency in management of the analyzed collections. The variation in the number of analyzed microsatellite loci has ranged from 8 in early studies (Hokanson et al., 2001) to 24 SSR loci in most recent studies (Lassois et al., 2016), with a notable exception of a study on Finnish and Swedish national collections, which relied on the data from eight SSR loci (Garkava-Gustavsson et al., 2013). Although the use of a higher number of SSRs increases the reliability of biostatistical analyses, Gross et al. (2012) have reported that less than 10 SSR loci were sufficient to determine potential duplicates among 1910 accessions in the U.S. Department of Agriculture *Malus* collection and likely from other large collections of *Malus* as well. Considering that molecular markers are employed to increase the financial sustainability of the conservation process (by identifying redundancies), the high cost of using an ever larger set of markers, in the analyses of big collections, is not always justified. Aside from accurately fingerprinting the collected accessions, SSR data can be used to investigate the underlying genetic structure and thus gain a much better insight into the examined germplasm. Although the use of a high number of SSR loci can identify even low differentiation within a population, Urrestarazu et al. (2015) report that in the strong structure and moderate differentiation situation, a minimum of eight SSRs is completely sufficient when analyzing *Pyrus* germplasm. Therefore, in this study, eight highly polymorphic SSR markers were selected to identify redundancies within six ex situ apple collections in Norway, as well as to investigate the genetic diversity and structure of the Norwegian apple germplasm.

Material and Methods

A total of 181 apple accessions (Supplemental Table 1), maintained in six ex situ collections located in western (Ulvik: 60°33'N 6°55'E and Njøs: 61°10'N 6°51'E)

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Table 1. Linkage group, number of detected alleles, effective number of alleles, number of rare alleles (frequency <0.05), allele size range, gene diversity (Nei, 1978), and probability of identity calculated for 158 apple accessions with unique SSR profile, maintained in six ex situ collections located in western and southeastern Norway.

Locus code	Linkage group no.	No. of alleles	Effective no. of alleles	No. of rare alleles	Size range (bp)	Gene diversity	Probability of identity
CH02C02b	4	4	1.93	2	97/113	0.48	0.371
CH04E02	4	10	4.72	5	138/166	0.79	0.075
CH02D08	11	15	4.49	10	203/254	0.78	0.078
CH01H01	17	11	5.66	5	105/141	0.82	0.049
CH01H02	9	14	4.80	9	227/257	0.79	0.076
CH01H10	8	10	3.31	5	85/119	0.70	0.125
CH05E03	2	20	4.98	16	153/198	0.80	0.068
CH05E04	16	11	6.36	4	150/176	0.84	0.048
Average		11.9	4.53			0.75	3.3 10^{-9}

and southeastern (Ås: 59°40'N 10°46'E, Dømmesmoen: 58°21'N 8°34'E, Landvik: 58°20'N 8°31'E, and Lier: 59°47'N 10°15'E) Norway were sampled for this study, along with 13 international, reference cultivars (Pink Lady, Topaz, Fuji Nagafu, Golden Reinders, Gala Galaxy, Pinova, Pilot, Jonagold, Piros, Braeburn, Melrose, Elstar, and Granny Smith) sampled from an ex situ collection in Bosnia and Herzegovina. Among the sampled accessions, most are considered traditional Norwegian cultivars, whereas some represent foreign cultivars with a longer or shorter tradition of cultivation in Norway. All accessions were genotyped using a set of eight SSR markers, previously used by Gaši et al. (2010, 2013b, 2013a) on traditional apple accessions from Bosnia and Herzegovina.

SSR analyses. Tissue samples for DNA analyses were collected in the autumn of 2014 and 2015, from a single tree for each accession. Genomic DNA was isolated from 70 to 80 mg of leaf powder using the CTAB method (Doyle and Doyle, 1987). Eight primer pairs (CH02C02b, CH04E02, CH02D08, CH01H01, CH01H02, CH01H10, CH05E03, and CH05E04), used for SSR amplifications have previously been published by Gianfranceschi et al. (1998) and Liebhard et al. (2002). None of the analyzed microsatellite markers were multilocus. Polymerase chain reaction (PCR) amplification of SSR sequences was performed in a Veriti TM Thermal Cycler (Applied Biosystems, Foster City, CA) using fluorescently labeled primers. All PCR amplifications were performed as described in Gianfranceschi et al. (1998). PCR product (1 µL) was added to a master mix containing 9 µL of deionized formamide and 0.5 µL GeneScan-350 Rox size-standard (Applied Biosystems). Samples were heated at 95 °C for 5 min and immediately cooled down on ice. The detection of SSR products was conducted on ABI 310 automated sequencer (Applied Biosystems). SSR profiles were scored using GeneMapper Software ID v3.2 (Applied Biosystems).

Biostatistical analyses. Population genetics software SPAGeDI 1.3 (Hardy and Vekemans, 2002) was used to calculate allele frequencies, the number of rare alleles per locus (alleles with frequency <0.05), effective number of alleles, and gene diversity (Nei, 1978). The probability of identity, as defined by Waits et al. (2001) was calculated

using GenAlEx ver. 6.5 (Peakall and Smouse, 2006). To examine the genetic structure and differentiation within the Norwegian apple germplasm, we used the Bayesian model-based cluster procedure within Structure version 2.2.3 (Pritchard et al., 2000). We computed *K* (unknown) reconstructed panmictic populations (RPPs) of individuals testing *K* (log-likelihood) = 1–10 for all accessions assuming that sampled cultivars were from unknown origin. Methodology described by Evanno et al. (2005) was used to estimate the most probable *K* value for the analyzed data. This was done through Structure harvester ver. 0.6. application (Earl and vonHoldt, 2011). Assignment of a cultivar in an RPP was provided by the probability of membership *q_i* chosen at 80% according to similar studies in apple (Gaši et al., 2013b; Urrestarazu et al., 2012). In addition, AMOVA (Excoffier et al., 1992) based on the stepwise mutation model, was calculated between the identified RPPs using GenoType software with 1000 permutations. The GenoType program is part of the GenoType/GenoDive package (Meirmans and Van Tienderen, 2004). A multivariate analysis, factorial correspondence analysis (FCA) based on allele frequencies was performed using Genetix 4.02 (Belkhir et al., 2001), which meant excluding all triploid genotypes.

Results and Discussion

SSR polymorphism. Eight primer pairs amplified 95 distinct alleles in this study, or on average 11.9 alleles per locus (Table 1). This is higher than the values published from similar studies on cultivated apple germplasm in Denmark (9.8) (Larsen et al., 2006), Sweden (10.3) (Garkava-Gustavsson et al., 2008), and Finland (8.8) (Garkava-Gustavsson et al., 2013). It is important to note that all except one (Garkava-Gustavsson et al., 2013) of the mentioned studies employed more than eight SSR markers. Slightly higher values have been reported on Spanish germplasm by Pereira-Lorenzo et al. (2007) (12.3). Much higher average number of alleles per SSR loci have been reported by van Treuren et al. (2010) (18.5), Urrestarazu et al. (2012) (16.7), Liang et al. (2015) (16.8), and Lassois et al. (2016) (19.5). However, the number of accessions included in the four mentioned studies ranged from 400 to above 2000. The average effective number of alleles in this

Table 2. List of synonym apple accessions found in six Norwegian ex situ collections using eight SSR primer pairs.

'Cellini' (Lier), 'Hampus' (Lier), and 'Husmor' (Lier)
'Gravenstein hollandsk' (Ulvik) and 'Hollandsk Gravenstein' (Dømmesmoen)
'Løkeple' (Njøs) and 'Silke-eple' (Njøs)
'Tommos' (Ås) and 'Keiserkrone' (Njøs)
'Simenraud' (Lier) and 'Melba raud' (Njøs)
'Lærdalseple' (Njøs) and 'Lavoll' (Njøs)
'Laxtons Exquisite' (Ulvik), 'Laxtons Superb' (Lier), and 'Lord Lambourne' (Ulvik)
'Prins' (Njøs) and 'Prins Kronprins' (Njøs)
'Ribston' (Lier) and 'Ribston Lagerod' (Dømmesmoen)
'Ekely' (Njøs) and 'Oster' (Njøs)
'Haustkavill' (Lier) and 'Kjerrigholm' (Lier)
'Langballe' (Njøs) and 'Kavill' (Ulvik)

study (4.53) was lower, but comparable to the values published on Finnish (4.66) (Garkava-Gustavsson et al., 2013) and Swedish (4.93) (Garkava-Gustavsson et al., 2008) apple germplasm. Even higher values have been reported by Urrestarazu et al. (2012) (6.69), Liang et al. (2015) (5.64), and Lassois et al. (2016) (6.2). The substantial difference between the average allele number and the average effective allele number in this study is probably due to a high presence of rare alleles (56 alleles or 59% of all detected alleles). High percentage of rare alleles indicates a presence of a considerable genetic diversity among the analyzed apple accessions, previously unused in breeding. The calculated gene diversity (0.75) (Table 1) was comparable to the value reported for Swedish apple germplasm (0.74) (Garkava-Gustavsson et al., 2008) and identical to the values published for the Finnish apple germplasm (Garkava-Gustavsson et al., 2013). Somewhat higher values for gene diversity have been reported by Urrestarazu et al. (2012) (0.82), Liang et al. (2015) (0.83), and Lassois et al. (2016) (0.82), however, on much larger set of samples. The highest value for probability of identity was calculated for CH02C02b (0.371), whereas the lowest for CH05E04 (0.048) (Table 1). Since the overall probability of identity was quite low (3.3×10^{-9}), the risk that two random accessions were erroneously assigned as identical is very unlikely.

Detection of more than two different alleles per locus, indicating a triploid state,

was observed for 22% or 12% of accessions from Norway (Supplemental Table 1). The percentage of genotypes with a third allele on one or more loci was comparable to the values reported by Garkava-Gustavsson et al. (2008) (10%) for the Swedish apple germplasm, but lower than 19% and 21% reported for the French (Lassois et al., 2016) and the Dutch (van Treuren et al., 2010) apple collections, respectively. Even higher percentage of these genotypes has been reported for apple germplasm maintained ex situ in northwestern (Pereira-Lorenzo et al., 2007)

(28%) and northeastern Spain (Urrestarazu et al., 2012) (24%), as well as for Bosnia and Herzegovina (Gaši et al., 2010, 2013b) (27%), which might indicate a higher presence of triploids among southern European germplasm compared with the Nordic ones.

Genetic identification. Overall, 14 cases of synonyms or possible mislabeling were detected (Table 2), of which eight were among accessions within individual collections, and the rest between accessions maintained at different sites. Several cases of homonyms or misleading names were also detected within the Norwegian apple collections ‘Astrakan gyllenkroks’, ‘Astrakan kvit’, and ‘Astrakan raud’ from Lier—although all three accessions have ‘Astrakan’ in their name, they are not genetically identical or even closely related. In addition, ‘Fuhr’ and ‘Fuhr raud’ from Njøs—the names suggest that ‘Fuhr raud’ is a red mutant of Fuhr cultivar. Indeed, they are closely related but not genetically similar enough to be considered clones (differences on three SSR loci). However, these two

accessions display differences in only one allele in each of the three loci, possibly indicating that ‘Fuhr red’ is an offspring of ‘Fuhr’. Out of four ‘Gravenstein’ apple accessions analyzed, ‘Gravenstein’ accession from Ulvik, with the attribute “hollandsk” (Dutch), is identical to ‘Hollandsk Gravenstein’ from Dømmesmoen. Meanwhile, ‘Gravenstein fusa’ from Njøs is not closely related to any of the other ‘Gravenstein’ accessions. Two ‘Laupsa-eple grønt’ accessions from Ulvik are completely unrelated genotypes; one of the ‘Lord Lambourne’ accessions from Dømmesmoen is not closely related to the other two analyzed ‘Lord Lambourne’ accessions (from Dømmesmoen and Ulvik); ‘Rosenstrip’ and ‘Rosenstrip Sogn’, both from Njøs, are in fact completely different genotypes, whereas ‘Vinterrosenstrips’ (Ulvik), was not identical or closely related to any of the other genotypes containing the name “Rosenstrip.” ‘Torstein gul’ from Ulvik is genetically completely different from ‘Stor Torstein’ and ‘Torstein raud’, both from Njøs.

Table 3. List of presumable mutants found in six Norwegian ex situ, which display identical genetic profiles obtained using eight SSR primer pairs.

‘Ingrid Marie’ (Lier) and ‘Ingrid Marie raud’ (Ås)
‘Prins’ (Njøs) and ‘Prins raud’ (Ås)
‘James Grieve’ (Lier) and ‘James Grieve, raud’ (Njøs)
‘Säsvstaholm’ (Lier) and ‘Säsvstaholm raud’ (Ulvik)
‘Stor Torstein’ (Njøs) and ‘Torstein raud’ (Njøs)

Fig. 1. Multivariate analysis (factorial correspondence analysis) of simple sequence repeat data for two defined reconstructed panmictic populations (RPPs) (only diploid genotypes with likelihood of membership to individual RPP above 80%).

The analyses of eight SSR loci revealed differences in one allele among the genetic profiles of 'Aroma' and 'Aroma raud' ('Aroma red'), as well as between 'Haugmann' (Ulvik) and 'Haugmann' (Njøs), indicating clonal polymorphism. On the other hand, several pairs of accessions, which are considered to be mutants, could not be differentiated using these SSR markers (Table 3).

Duplicates in ex situ collections (accessions carrying the same name and which have the same SSR profile) were few: 'Åkerø hassel' (Lier), 'Åkerø', and 'Åkerø hassel' (both from Ulvik) all have the same names and also have an identical genetic profile; 'Lord Lambourne' from Ulvik and one of the accessions registered as 'Lord Lambourne' from Dømmesmoen have an identical genetic profile; two 'Silke-eple', from Njøs and Lier collection, respectively, have identical names and have an identical genetic profile. It is important to note that properly identified duplicate accessions, maintained in more than one collection, can be useful as reference genotypes, as well as safety backups.

Out of 181 analyzed accessions, from six ex situ collections located in western and south-eastern Norway, 158 displayed a unique SSR profile. The identified percentage of redundancies (13%), in this study, is lower than what has been reported for apple collections in the Netherlands (van Treuren et al., 2010) (32%), Spain (Urrestarazu et al., 2012) (47%), Italy (Liang et al., 2015) (34%) and France (34%) (Lassois et al., 2016), but equal to the values reported by Gaši et al. (2013b) (13%). Although the redundancy does not appear to be a major issue within the analyzed Norwegian collections, the use of SSR markers has identified all the mislabeled accessions, which should contribute to a more efficient management of the collected germplasm. The process of renaming the mislabeled accessions will be aided by available passport data. Also, a morphological reevaluation of suspected synonyms needs to be conducted before removing any of the accessions from the collections.

Genetic structure. Bayesian analyses of 194 accessions (181 accessions from Norwegian ex situ collections and 13 international, reference cultivars) was conducted using Structure. Subsequent ΔK analyses (Evanno et al., 2005) revealed a maximum value for $K = 2$, with no additional substructuring within the two identified RPPs. Overall, 62 accessions clustered in RPP1 and 76 in RPP2, whereas 56 accessions were admixed (did not adhere to any of the two RPPs with the probability of membership above 80%) (Supplemental Table 1). RPP1 consisted mainly of traditional Scandinavian cultivars, but notably included some very winter-hardy cultivars such as Charlamovsky, Gravenstein, Transparente Blanche, and Wealthy.

Twelve of the 13 international, reference cultivars clustered inside RPP2. Numerous old apple cultivars introduced to Norway from western Europe and North America ('Beauty of Bath', 'Belle de Boskoop', 'Cox's Orange', 'Jacques Lebel', 'James

Grieve', 'Laxtons Superb', 'Lord Lambourne', 'Summerred', 'Wagener', 'Worcester Pearmain', etc.) also grouped within the same RPP. Foreign apple germplasm had a significant presence among the admixed accessions ('Bramleys seedling', 'Dunelow seedling', 'Early McIntosh', 'Early Red Bird', 'Geneva Early', etc.), including one of the international, reference cultivars (Fuji Nagafu). The genetic differentiation between the two identified RPPs was examined using AMOVA. AMOVA detected that most of the variance was retained within the RPPs (92.3%), whereas 7.7% of the total diversity was attributed to the differences among the analyzed groups of accessions. The obtained values for AMOVA were significant ($f_{CT} = 0.077$; $P < 0.01$). To get a clearer picture of the genetic relationships between the analyzed RPPs, a FCA was performed. The separation between the two clusters (Fig. 1) was evident and thus the FCA confirmed results obtained by AMOVA.

No correlation was found between the geographical location of the individual accession and their RPP distribution. However, large presence of foreign apple cultivars introduced from southern countries within RPP2, together with a dominant occurrence of traditional Scandinavian and very winter-hardy cultivars within RPP1, indicates that climate adaptation may have contributed significantly to the genetic structure of the analyzed germplasm. The effect of climate adaptation on genetic structure of apple germplasm was previously hypothesized by Garkava-Gustavsson et al. (2013) in a study on Finish and Swedish national apple collections.

Conclusion

Using eight polymorphic SSR markers, we managed to identify a number of mislabeled accessions, as well as duplicates, among apple accessions conserved within six ex situ collections located in Norway, which should contribute to a more efficient management of the collected germplasm. It is necessary to rename the mislabeled accessions to avoid future confusion. Available passport data should help in this process.

The results of the Bayesian analyses do not indicate a strong differentiation between the foreign and the Norwegian apple accessions; however, there is some evidence that the climate adaptation has influenced the genetic structure of the examined germplasm. On the basis of the low occurrence of redundancies and calculated diversity parameters, apple accessions currently maintained ex situ in Norway represent a diverse germplasm which could be very valuable in future breeding programs, especially for the Scandinavian climate.

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Supplemental Table 1. SSR profiles and ploidy of 181 apple accessions, maintained in six ex situ collections located in Norway, and 13 international, reference cultivars, analyzed in this study using eight SSR markers, as well as assignment of each genotype to a reconstructed population ($K = 2$) defined by Structure (Pritchard et al., 2000) (probability of membership $q_i > 80\%$).

Apple accessions	Collection	Ploidy	CH02C02b	CH04E02	CH02D08	CH01H01	CH01H02	CH01H10	CH05E03	CH05E04	$K = 2$
Norwegian collections											
Akero "Hassel"	Lier	2n	109:113	142:158	212:212	113:117	239:247	102:107	163:163	160:160	0
Alice	Lier	2n	109:109	154:158	212:254	113:117	235:247	105:113	172:172	154:154	1
Aroma	Lier	2n	109:109	144:158	212:212	119:121	235:247	091:102	172:172	154:160	0
Aroma, raud	Lier	2n	109:109	144:158	212:212	119:121	235:247	091:102	170:170	154:160	0
Astrakan, Gyllenkroks	Lier	2n	109:113	154:154	225:254	117:117	235:247	102:105	163:163	154:170	1
Astrakan, kvit	Lier	2n	109:109	154:154	212:254	115:115	235:235	095:102	176:176	160:170	1
Astrakan, raud	Lier	2n	109:109	150:150	212:225	119:121	235:235	102:113	189:189	162:168	0
Cellini	Lier	2n	109:113	150:158	212:212	115:117	235:235	102:102	162:162	162:162	1
Cox's Orange	Lier	2n	109:113	150:150	212:254	119:129	243:247	102:102	172:172	154:168	2
Cox's Pomona	Lier	2n	109:109	156:156	218:218	113:129	243:247	102:113	163:172	160:168	2
Eldrau/Ildrod Pigeon	Lier	2n	113:113	150:158	203:225	115:121	235:247	102:109	163:165	154:164	0
Filippa	Lier	2n	109:109	144:158	212:212	121:131	235:235	091:102	163:163	154:160	0
Gräygilling	Lier	2n	109:109	150:150	212:212	117:129	249:249	102:107	163:163	160:160	0
Gul Richard	Lier	2n	113:113	152:158	203:229	121:121	247:249	102:113	164:168	160:168	2
Hampus	Lier	2n	109:113	150:158	212:212	115:117	235:235	102:102	163:163	162:162	1
Hauskavill	Lier	2n	109:109	158:158	218:225	117:119	235:243	095:102	165:191	154:168	2
Husmor	Lier	2n	109:113	150:158	212:212	115:117	235:235	102:102	163:163	162:162	1
Ingrid Marie	Lier	2n	109:109	150:158	254:254	113:119	247:247	102:113	172:172	154:160	2
James Grieve	Lier	2n	113:113	150:154	229:229	119:119	247:247	102:102	163:172	160:168	2
Jens Pedersen	Lier	2n	109:109	158:158	212:212	113:119	235:235	107:107	163:172	160:162	0
Jens Pedersen	Lier	2n	109:109	158:158	218:218	117:121	247:253	095:102	163:163	158:176	2
Katja	Lier	2n	113:113	150:158	212:229	119:131	247:247	102:102	163:191	162:168	2
Kjerringholm	Lier	2n	109:109	158:158	218:225	117:119	235:243	095:102	165:191	154:168	2
Lamyreple	Lier	2n	109:109	142:158	254:254	113:115	235:247	107:113	163:163	162:164	0
Laxton's Superb	Lier	2n	113:113	150:150	218:218	129:131	247:251	102:102	172:172	154:168	2
Lobo	Lier	2n	113:113	142:158	229:254	113:117	235:247	102:102	172:172	150:150	2
Ribston	Lier	3n	109:113	150:158	225:229	119:131:141	243:247	102:102	163:172	160:164:168	2
Sävsstaholm	Lier	2n	109:109	154:154	212:254	115:129	235:239	102:105	163:163	164:170	1
Signe Tillisch	Lier	2n	109:109	158:158	212:218	113:119	235:235	102:107	163:172	162:162	0
Silke-eple	Lier	2n	113:113	150:158	212:225	113:115	247:247	102:109	172:172	154:160	2
Simenrud	Lier	2n	113:113	154:166	212:254	113:113	245:247	102:107	172:172	158:160	2
Sorneseple	Lier	2n	109:109	154:158	254:254	115:121	235:253	102:105	176:182	154:160	2
Summerred	Lier	2n	113:113	154:158	212:229	115:119	235:247	102:113	170:184	168:168	2
Tohoku	Lier	2n	113:113	140:158	212:212	115:131	247:247	095:102	163:163	158:160	0
Transparente Blanche	Lier	2n	109:109	150:150	216:225	113:115	235:235	102:107	163:172	170:170	1
Benoni	Ås	2n	109:109	158:158	212:229	119:119	247:247	095:102	186:186	154:160	2
Bramley's Seedling	Ås	3n	109:113	158:158	212:212	117:121	235:235	102:102	153:153	150:160:168	0
Close	Ås	3n	109:113	150:150	216:254	115:115	235:243	095:107	172:172	154:160:170	0
Early McIntosh	Ås	2n	109:113	150:166	212:216	115:117	235:247	102:107	163:163	158:158	0
Ingelin	Ås	2n	109:113	144:154	212:212	115:119	245:247	102:107	163:163	160:160	0
Ingrid Marie, raud	Ås	2n	109:109	150:158	254:254	113:119	247:247	102:113	172:172	154:160	2
Karina	Ås	2n	109:109	154:158	212:254	119:121	247:247	102:102	163:163	154:160	0
Kjølberggeple	Ås	3n	109:113	138:144	254:254	113:113	235:235	095:102:105	163:163	164:168	1
Linda	Ås	2n	109:109	138:150	212:254	115:119	-	102:102	163:176	168:168	1
Mariann	Ås	2n	113:113	150:154	212:254	115:121	247:247	095:102	172:172	160:168	2
Sota-Kari	Ås	2n	109:113	142:154	212:212	115:121	245:247	095:102	170:170	160:160	0
Sylvia	Ås	2n	113:113	154:158	252:252	117:131	247:247	102:102	162:162	162:162	2
Tommos	Ås	3n	109:113	144:150	212:225	113:113	235:245	095:102:113	172:172	150:176	2
Virginsk Roseneple	Ås	2n	109:109	150:154	212:216	113:113	235:235	102:105	172:172	170:170	1
Prins, raud	Ås	2n	109:109	158:158	212:223	113:113	247:247	109:111	165:165	162:176	0

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Supplemental Table 1. (*Continued*) SSR profiles and ploidy of 181 apple accessions, maintained in six ex situ collections located in Norway, and 13 international, reference cultivars, analyzed in this study using eight SSR markers, as well as assignment of each genotype to a reconstructed population ($K = 2$) defined by Structure (Pritchard et al., 2000) (probability of membership $q_i > 80\%$).

Apple accessions	Collection	Ploidy	CH02C02b	CH04E02	CH02D08	CH01H01	CH01H02	CH01H10	CH05E03	CH05E04	$K = 2$
Antonovka	Njøs	2n	109:109	158:166	248:248	115:115	235:247	085:085	189:189	168:168	0
Apalseteple	Njøs	2n	109:109	150:154	225:254	121:121	235:235	085:105	172:172	154:160	1
Bente	Njøs	2n	113:113	154:166	212:229	115:121	235:247	085:102	170:172	168:168	2
Bismarck	Njøs	2n	109:109	154:158	218:254	113:113	243:245	102:107	172:172	160:162	2
Dr. Nansen	Njøs	3n	109:113	154:166	248:254	115:115	235:247	085:095:102	176:189	160:168	0
Edholm	Njøs	2n	113:113	152:158	212:229	115:121	247:247	105:105	172:191	160:160	2
Eir	Njøs	2n	109:109	158:158	229:254	115:119	235:247	102:102	174:191	168:168	2
Franskar	Njøs	2n	113:113	144:156	214:218	117:119	235:235	102:109	167:189	160:160	0
Ekely	Njøs	2n	113:113	150:166	225:248	113:131	235:247	095:102	174:174	168:168	2
Flaske-eple	Njøs	2n	109:113	144:154	212:254	119:119	235:247	095:102	172:172	154:160	2
Fosseple	Njøs	2n	109:109	150:166	225:248	113:113	235:235	102:109	167:167	160:162	0
Fuhr	Njøs	2n	113:113	158:158	225:225	115:115	235:247	085:102	163:172	164:176	0
Fuhr, raud	Njøs	2n	113:113	158:158	225:225	115:119	235:247	102:107	163:172	176:176	2
Glopestadeple	Njøs	2n	109:109	150:154	212:225	113:115	235:251	105:109	172:176	160:176	1
Gravenstein	Njøs	2n	109:109	144:150	225:254	115:115	235:239	095:102	163:189	160:174	1
Gravenstein Fusa	Njøs	3n	109:109	154:158	214:254	115:121	235:249	095:102:107	172:176:189	154:170	1
Grindseple	Njøs	2n	109:113	158:166	214:214	115:131	247:255	102:107	153:163	160:176	0
Haugeple	Njøs	3n	109:109	154:154	212:225	115:117:121	227:237:251	095:102:109	163:172:176	160:168	1
Haugmann	Njøs	2n	109:113	140:154	225:225	117:117	235:235	105:109	172:172	170:174	1
Håkonseple	Njøs	2n	109:109	158:158	225:254	121:121	247:251	102:109	172:172	154:160	0
Hindals dromming	Njøs	2n	109:109	158:158	212:225	113:131	243:247	102:107	163:191	160:168	2
Høyenes	Njøs	2n	109:109	144:144	212:225	117:131	235:243	095:102	165:191	176:176	0
Idum	Njøs	2n	113:113	154:158	229:254	119:121	245:247	102:102	163:191	168:168	2
Rød James Grieve	Njøs	2n	113:113	150:154	229:229	119:119	247:247	102:102	163:172	160:168	2
Jordbareple	Njøs	2n	109:113	144:150	212:225	113:131	245:245	102:103	163:163	176:176	2
Katinka	Njøs	2n	113:113	158:166	212:229	121:131	245:247	095:102	172:191	160:168	2
Kaupanger	Njøs	2n	113:113	144:150	212:225	113:115	235:247	102:109	172:172	160:160	2
Keiserkrone	Njøs	3n	109:113	144:150	212:225	113:113	235:245	095:102:113	172:172	150:176	2
Langballe	Njøs	2n	109:113	154:156	214:254	117:117	235:235	095:109	176:189	170:170	1
Laveple	Njøs	2n	109:109	154:166	212:254	115:115	235:235	105:109	170:170	160:174	1
Lavoll	Njøs	2n	109:109	150:158	254:254	113:121	235:235	102:109	163:172	154:164	1
Lærdalseple	Njøs	2n	109:109	150:158	254:254	113:121	235:235	102:109	163:172	154:164	1
Leiknes	Njøs	3n	109:109	154:158	212:254	115:115	249:253	095:102:109	163:174	154:162	1
Leinestrand	Njøs	3n	109:109	138:154	203:212	115:117	233:235	095:105:109	163:172	154:160	1
Leriseple	Njøs	3n	109:109	144:158	218:225	115:115	235:241	095:102:109	172:172	164:176	0
Løeple	Njøs	2n	109:109	144:150	212:254	117:119	233:235	095:109	165:172	154:154	1
Løkeple	Njøs	2n	113:113	150:158	212:225	113:115	247:247	102:109	172:172	154:160	2
Marta-eple	Njøs	2n	109:113	150:158	212:254	113:119	247:251	102:102	163:163	164:176	0
Melba, raud	Njøs	2n	113:113	154:166	212:254	113:113	245:247	102:107	172:172	158:160	2
Mostereple	Njøs	3n	109:109	144:144	212:225	113:117	235:251	095:109	191:191	154:168:176	0
Nanna	Njøs	3n	109:113	154:158	212:229:254	115:115	235:247	095:102	172:174	164:170	0
Nordfjordeple	Njøs	2n	109:109	158:158	218:225	113:113	235:235	095:107	172:172	160:176	0
Olinaeple	Njøs	2n	109:113	154:154	203:254	115:115	235:235	102:102	176:176	154:160	1
Oranie	Njøs	2n	109:109	156:166	203:248	115:117	235:235	095:105	163:172	160:176	1
Oster	Njøs	2n	113:113	150:166	225:248	113:131	235:247	095:102	174:174	168:168	2
Pederstrup	Njøs	2n	109:113	138:144	212:254	113:131	247:247	102:113	172:172	160:168	2
Petrineeple	Njøs	2n	109:113	144:154	212:225	113:115	235:247	095:095	176:176	160:176	1
Prins	Njøs	2n	109:109	158:158	212:223	113:113	247:247	109:111	165:165	162:176	0
Prins 'Kronprins'	Njøs	2n	109:109	158:158	212:223	113:113	247:247	109:111	165:165	162:176	0
Riskedal	Njøs	2n	109:109	144:154	203:212	115:115	235:247	095:102	163:170	154:160	1
Rival	Njøs	3n	109:109	158:158	212:225	111:113	239:251	095:102:109	163:163	174:176	1

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Supplemental Table 1. (Continued) SSR profiles and ploidy of 181 apple accessions, maintained in six ex situ collections located in Norway, and 13 international, reference cultivars, analyzed in this study using eight SSR markers, as well as assignment of each genotype to a reconstructed population ($K = 2$) defined by Structure (Pritchard et al., 2000) (probability of membership $q_i > 80\%$).

Apple accessions	Collection	Ploidy	CH02C02b	CH04E02	CH02D08	CH01H01	CH01H02	CH01H10	CH05E03	CH05E04	$K = 2$
Rondstveit	Njøs	2n	109:109	158:166	212:225	113:131	235:247	095:102	163:163	168:176	2
Rosenstrips	Njøs	2n	109:109	158:166	212:225	115:127	235:247	095:102	172:172	168:176	2
Rosenstrips, Sogn	Njøs	3n	113:113	144:158	212:225	113:127:129	235:247	102:107	172:172	160:176	2
Silke-eple	Njøs	2n	113:113	150:158	212:225	113:115	247:247	102:109	172:172	154:160	2
Siv	Njøs	2n	113:113	158:158	212:254	119:127	235:247	095:102	174:191	168:168	2
Steinkyrkje	Njøs	2n	109:109	150:154	218:254	113:131	243:243	102:102	172:172	154:162	2
Stor Torstein	Njøs	2n	113:113	158:158	212:225	113:119	235:247	095:102	172:172	160:176	2
Stølen	Njøs	2n	113:113	144:158	212:225	115:131	235:247	095:102	191:191	162:168	2
Susanna	Njøs	2n	113:113	154:166	212:254	119:127	247:247	095:102	163:172	160:168	2
Svensk Rosenhäger	Njøs	2n	109:113	144:152	212:212	121:127	235:247	095:102	172:191	160:160	2
Sylfesteple	Njøs	2n	109:109	142:166	212:254	115:129	247:247	102:102	163:189	154:154	0
Tolleivseple	Njøs	2n	109:113	150:158	212:218	115:115	245:247	102:109	163:172	160:160	2
Torstein raud	Njøs	2n	113:113	158:158	212:225	113:119	235:247	095:102	172:172	160:176	2
Tveiteple	Njøs	2n	109:113	158:158	212:225	115:115	235:235	095:102	163:163	168:168	0
Vete	Njøs	2n	109:109	158:158	212:212	117:121	235:247	105:109	172:172	154:160	1
Vägenepile	Njøs	2n	109:109	154:166	248:248	105:105	235:245	095:095	180:182	150:154	0
Wagener	Njøs	2n	109:109	144:158	212:225	117:131	245:247	095:102	172:198	150:164	2
Wealthy	Njøs	2n	109:109	154:154	212:212	115:115	247:255	095:102	176:184	160:168	1
Øskang	Njøs	2n	109:109	144:154	212:212	115:115	235:235	102:102	191:191	160:168	0
Øysteinseple	Njøs	2n	109:109	154:158	218:254	113:121	237:253	102:105	172:172	160:162	1
Aagtoeple	Njøs	2n	113:113	152:154	254:254	113:115	235:247	103:109	163:176	160:160	1
Guldborg	Dommesmoen	3n	109:109	144:150:154	212:225:254	115:131	235:239	095:102	163:190	160:174	1
Halling	Dommesmoen	2n	113:113	158:166	212:254	117:121	249:249	102:113	163:163	160:168	0
Hollandsk Gravenstein	Dommesmoen	2n	109:109	150:158	254:254	113:119	237:253	102:109	163:172	154:164	1
Lord Lambourne	Dommesmoen	2n	113:113	150:150	218:218	129:131	247:251	102:102	172:172	154:168	2
Lord Lambourne	Dommesmoen	2n	113:113	150:158	212:252	113:121	249:249	102:102	172:192	164:168	2
Ribston Lägrød	Dommesmoen	3n	109:113	150:158	225:229	119:131:141	243:247	102:102	163:172	160:164:168	2
Rod Ananas	Dommesmoen	2n	109:113	154:158	206:206	115:121	237:249	102:113	163:163	154:176	1
Grefstadepile	Landvik	2n	109:113	154:154	214:254	115:115	237:237	095:109	174:190	170:170	1
Landvikeple	Landvik	2n	113:113	150:158	212:254	113:117	237:237	095:095	153:161	164:168	1
Trokhals	Landvik	2n	109:113	154:154	229:254	115:131	237:245	095:095	163:172	160:164	0
Åkerø	Ulvik	2n	109:113	142:158	212:212	113:117	239:247	102:107	163:163	160:160	0
Åkerø "Hassel"	Ulvik	2n	109:113	142:158	212:212	113:117	239:247	102:107	163:163	160:160	0
Arreskov	Ulvik	2n	109:113	154:166	212:225	115:127	235:243	095:095	172:172	160:168	2
Beauty of Bath	Ulvik	2n	109:113	144:166	225:229	117:117	235:245	102:102	184:184	154:176	2
Belle de Boskoop	Ulvik	2n	109:113	152:154	212:225	105:127	243:243	095:102	178:178	160:168	2
Björgvin	Ulvik	2n	109:109	154:158	225:254	115:115	235:235	102:105	161:163	170:170	1
Borsdorfer	Ulvik	2n	109:113	150:158	212:225	113:121	237:253	102:109	170:170	160:176	1
Brudgomseple	Ulvik	2n	113:113	144:158	218:225	115:119	237:237	102:109	190:190	176:176	1
Brureple	Ulvik	3n	109:109	158:158	212:227:246	115:115	237:249	102:111	165:165	162:162	1
Charlamovsky	Ulvik	2n	109:113	154:154	212:254	113:115	235:255	102:102	176:176	168:168	1
Charles Ross	Ulvik	2n	109:109	150:154	212:254	119:119	237:249	102:102	154:162	154:162	1
Dunelow seedling	Ulvik	2n	109:109	150:158	212:254	119:131	237:237	102:102	163:163	168:168	0
Early Red Bird	Ulvik	2n	113:113	154:154	212:212	115:119	233:237	102:102	174:174	168:168	0
Enestående	Ulvik	2n	111:111	144:154	227:254	115:117	235:235	095:102	176:191	168:176	0
Fristeren	Ulvik	2n	109:109	150:154	212:225	113:115	237:253	102:109	168:176	168:168	1
Furuholm	Ulvik	2n	109:113	154:158	212:212	127:129	235:235	102:119	163:163	154:164	0
Garborg	Ulvik	2n	113:113	144:158	212:225	115:115	245:247	095:102	172:189	154:176	2
Geneva Early	Ulvik	2n	113:113	154:154	212:212	115:121	245:249	102:107	163:176	158:158	0
Granat	Ulvik	2n	109:109	158:158	212:225	113:113	239:251	102:107	163:163	170:176	1
Gravenstein, hollandsk	Ulvik	2n	109:109	150:158	254:254	113:119	237:253	102:109	163:172	154:164	1

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Supplemental Table 1. (*Continued*) SSR profiles and ploidy of 181 apple accessions, maintained in six ex situ collections located in Norway, and 13 international, reference cultivars, analyzed in this study using eight SSR markers, as well as assignment of each genotype to a reconstructed population ($K = 2$) defined by Structure (Pritchard et al., 2000) (probability of membership $q_i > 80\%$).

Apple accessions	Collection	Ploidy	CH02C02b	CH04E02	CH02D08	CH01H01	CH01H02	CH01H10	CH05E03	CH05E04	$K = 2$
Gullspir	Ulvik	2n	113:113	158:158	229:229	117:121	249:253	119:119	163:163	168:168	2
Haugmann	Ulvik	2n	109:113	140:154	212:225	117:117	235:235	105:109	170:172	170:174	1
Heimvik	Ulvik	2n	109:109	154:156	212:212	117:117	237:237	102:105	170:176	150:170	1
Hjartnes	Ulvik	2n	109:109	150:158	212:225	113:117	249:249	102:109	165:165	150:154	0
Jacques Lebel	Ulvik	2n	109:109	144:152	212:212	121:127	235:243	095:102	178:178	168:168	2
Kavill	Ulvik	2n	109:113	154:156	214:254	117:117	235:235	095:109	176:189	170:170	1
Knuteple	Ulvik	2n	109:109	150:158	212:225	115:127	235:235	095:102	172:172	164:164	0
Krekke-eple	Ulvik	2n	109:113	150:150	212:246	113:119	237:237	102:102	163:176	154:154	1
Kviteple	Ulvik	2n	113:113	144:150	212:225	115:115	249:257	102:109	172:174	154:154	0
Laupsa-eple, grønt	Ulvik	2n	109:109	156:158	214:254	117:117	249:249	102:111	172:172	154:160	1
Laupsa-eple, grønt	Ulvik	2n	109:113	158:158	214:225	115:115	249:249	102:102	163:163	154:160	1
Laxton's Exquisite	Ulvik	2n	113:113	150:150	218:218	129:131	247:251	102:102	172:172	154:168	2
Lord Lambourne	Ulvik	2n	113:113	150:150	218:218	129:131	247:251	102:102	154:168	172:172	2
Maglemer	Ulvik	3n	109:109	140:150	212:225	113:115	235:239:243	105:109	172:184	160:170	1
Rosenrød	Ulvik	2n	109:109	158:166	212:227	115:131	237:249	095:102	-	168:176	1
Rossvoll	Ulvik	3n	109:113	154:166	212:225:254	115:115	237:251	095:102:109	170:176:190	154:162:170	1
Savstaholm, raud	Ulvik	2n	109:109	154:154	212:254	115:129	235:239	102:105	163:163	164:170	1
Sitroneple	Ulvik	2n	109:109	154:158	212:216	113:117	237:237	102:102	172:190	160:162	1
Sommerkavill	Ulvik	2n	109:109	138:150	206:212	121:141	237:249	102:113	163:190	166:170	1
Storesteinseple	Ulvik	3n	109:113	158:158	212:225:229	113:115	235:245	102:102	161:165	154:154	0
Strutar	Ulvik	2n	109:109	150:158	212:254	113:121	237:253	102:109	173:172	154:164	1
Sukkerple	Ulvik	2n	109:109	150:158	212:225	115:121	247:251	102:102	162:172	154:160	0
Sysekavill	Ulvik	2n	109:109	144:154	212:254	115:131	237:237	095:102	165:176	160:160	1
Teigeple	Ulvik	2n	109:109	158:158	225:225	115:131	235:239	102:102	163:163	168:168	0
Torstein, gul	Ulvik	2n	113:113	158:158	212:225	115:121	237:249	102:102	172:172	160:176	0
Ulgenes	Ulvik	2n	109:113	144:158	212:212	115:115	235:239	102:102	163:163	168:168	0
Vinterrosenstrips	Ulvik	2n	109:109	158:166	212:229	113:121	245:249	095:113	157:172	160:160	2
Vista Bella	Ulvik	2n	113:113	150:158	254:254	115:117	235:247	095:102	163:172	158:176	0
Worcester Pearmain	Ulvik	2n	109:109	144:158	212:212	113:113	247:247	102:107	191:191	168:168	2
International reference cultivars											
Pink Lady		2n	109:109	158:158	212:223	113:119	235:249	095:102	167:178	160:164	2
Topaz		2n	109:109	150:158	250:254	119:121	247:247	102:102	184:191	162:168	2
Fuji Nagafu		2n	109:113	154:158	212:212	117:117	245:247	095:102	163:189	164:168	0
Golden Reinders		2n	113:113	158:158	223:225	117:119	247:249	095:113	178:184	160:168	2
Gala Galaxy		2n	113:113	152:158	225:254	119:131	235:247	095:113	172:184	164:168	2
Pinova		2n	113:113	158:158	218:223	119:131	247:249	106:113	172:178	160:162	2
Pilot		2n	113:113	154:158	254:254	115:121	247:251	095:102	163:172	168:168	2
Jonagold		3n	109:113	150:158	223:225:229	117:119:131	247:249	095:113	163:178:184	160:168	2
Piros		2n	113:113	150:150	216:229	113:121	243:247	098:100	172:172	168:172	2
Braeburn		2n	113:113	154:158	218:254	117:131	235:235	100:102	189:189	160:168	2
Melrose		2n	109:113	150:152	212:229	115:117	245:247	095:102	164:189	160:168	2
Elstar		2n	113:113	158:158	223:254	113:119	247:247	113:113	163:178	153:160	2
Granny Smith		2n	109:109	154:158	212:250	113:131	243:245	100:102	167:180	149:160	2