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In situ and ex situ assessment of morphological and fruit variation in Scandinavian sweet cherry

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Abstract

Sweet cherry is a tall, deciduous tree producing stone fruits. This diploid outcrossing species was domesticated in Asia but has been grown in orchards and home gardens in Scandinavia for many years. In situ and ex situ assessments of phenotypic variation in sweet cherry accessions were performed to determine the reliability of such assessments, and to determine relationships between Nordic populations. Principal component analysis (PCA) based on in situ data revealed that accessions were mostly clustered according to their country of origin. PCA based on ex situ assessment of accessions that were propagated by seed at Hornun (Denmark) did not agree with the PCA based on in situ data. These contrasting results suggest that phenotypic assessment in sweet cherry depends on the environment, genotype, and the interaction between them. Phenotypic diversity accounted for by in situ assessment may not be always true, while phenotypic differences determined by ex situ assessment may be confounded by the genotype-by-environment interaction, or could depend on the new genotypes arising from open pollination after seed propagation. Our research also suggests that ecotype differentiation could occur in wild Scandinavian sweet cherry. Fruit descriptors were among the best to distinguish between Scandinavian populations. Previously reported monogenic characteristics showed intermediate narrow-sense heritability, as suggested by the percentage of total variation accounted by the half-sib populations.

Keywords: *Prunus avium*; Conservation genetic resources; Phenotypic diversity

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1. Introduction

Sweet cherry (*Prunus avium* L.) was domesticated in Central Asia, but nowadays trees of this species are observed growing wild in most of Europe and nearby Asia, particularly in northern Iran and Ukraine (Webster, 1996). The species, which may be seed propagated but is self-incompatible, becomes rare towards the north because of its sensitivity to cold winters (Dahl, 1988a). The tree, which is vigorous and can be 20 m tall, is mostly found in single tree stands or in small groups.

According to Dahl (1988b), sweet cherry cultivation seems to be very old. The Roman writer Varro (116–27 B.C.) described its grafting technique, while Pliny (23–79 A.D.) provided information for eight distinct cultivars. Findings in Norwegian graves revealed that cherries were part of the Scandinavian diet 1500 years ago (Shübeler, 1888). Sweet cherry cultivation started in Scandinavia during the Middle Ages. Probably the first domestication occurred in this region by moving promising wild individuals into gardens. Sweet cherry regenerates well in natural habitats. Both young seedlings (raised from cross-pollination) and suckers (genetically identical with the mother tree) can be easily transplanted.

Some of the cherry cultivars grown today are either old local cultivars or their next generation, e.g. in eastern Europe and the former USSR (Iezzoni et al., 1990). According to Bargioni (1996) sweet cherry, as compared to other fruit species, exhibit high genetic variability, which has not yet been well explored and exploited. Iezzoni et al. (1990) also indicated that knowledge about the inheritance of horticulturally important characteristics is limited. Hence there is a need for a systematic assessment of cultivars and wild germplasm for specific characteristics.

The European Cooperative Programme for Conservation and Exchange of Crop Genetic Resources (ECP/GR) and the International Board for Plant Genetic Resources (IPBGR, now IPGRI) started collaborative European genebank research on *Prunus* at the beginning of the 1980s (Schmidt, 1985). It was recommended that wild forms, landraces and old cultivars should be described. An update of this work has been provided by Gass et al. (1996), recently. So far the ECP/GR has focused mainly on cultivar description.

Research to obtain more knowledge about the geographic distribution and the biological variation in the Nordic gene pool of wild sweet cherry was performed by the Nordic Gene Bank (Fernqvist, 1996). The aims of our paper were to carry out analyses on in situ data and ex situ assessment of the accessions available in the Nordic Gene Bank, to determine the reliability of such assessments, and to determine the relationships between Nordic populations. This paper provides analyses of data collected from 36 populations of wild mother trees in Sweden, Norway and Bornholm (southern Denmark), and from data recorded in a second open-pollinated generation from some of these mother trees.

2. Materials and methods

2.1. In situ assessment

Based on Nordic floras (Lagerberg, 1947; Lagerberg and Holmboe, 1939; Shübeler, 1888) and local horticultural expertise, areas with wild sweet cherry trees were identified and listed. In Sweden the species spreads from Scania (south) to Uppland, Dalarna, and Värmland (north). Small populations (1–3 trees) were described at 30 locations, the southernmost being Baskemölla (55°14′) and the northenmost at Tullgarn (59°18′). The trees were mostly found on flat and cultivated land. Among the Danish islands, Bornholm (55°15′) is well known for sweet cherry growing, and was therefore chosen for the inventory. Mother trees in small populations (1–4 trees) were described at four different locations. The environment where these trees were growing was an undulating pasture. In Norway sweet cherry is found in the southern lowland areas, specially near the Oslo fiord and along the coast. In our analysis we used mother trees from two different populations, one near Jeløy in the Oslo district (59°10′) and the other near Grimstad (58°8′). There were 19 trees per population. In Jeløy the trees were mostly found near field borders, while the growing sites in Grimstad were characterized by forests and slopes. The shortest distance between the locations of Norwegian and Swedish accessions was approximately 300 km. The Danish accessions were isolated on the island of Bornholm (50 km away from the nearest mainland).

At the time of fruit ripening (July–August) the mother trees were characterized with descriptors recommended for in situ morphological variation (Table 1). The Danish and Swedish accessions used were described in 1982 or 1985, while the Norwegian accessions were described in 1993.

Table 1
Descriptors considered for the in situ morphological variation between 36 Scandinavian populations of sweet cherry

Descriptor	Scale
Shrub/tree height	m
Habitus 1	1 = tree, 2 = shrub, 3 = tree with more than one stem
Habitus 2	1 = erect, 2 = spreading, 3 = drooping
Fruit size	mm
Fruit set	1 = none, 2 = weak, 3 = medium, 4 = heavy
Fruit colour	1 = yellow, 2 = orange-yellow, 3 = red on pale yellow ground, 4 = red, 5 = purple, 6 = black
Fruit taste	1 = very acid, 2 = acid, 3 = intermediate, 4 = sweet, 5 = very sweet
Fruit flesh colour	1 = whitish, 2 = pink, 3 = red, 4 = purple
Stone size	mm

2.2. Ex situ assessment

Seeds collected from open-pollinated mother trees in 1985 were sown in spring 1986. The seeds germinated well in autumn 1987, and 1680 seedlings were planted in eight rows in an experimental field at Hornum (Denmark). The planting distance within the rows was approximately 1 m and between rows 5 m. The seedlings derived from open-pollinated seed collected from eight mother trees grown at three locations in Bornholm, and 20 mother trees grown at seven locations in southern Sweden.

After eight growing seasons berries were observed on most trees. The half-sib populations were thus characterized in August 1995, May 1997 and August 1997. There were 300 Danish derived seedlings (20–60 half-sibs per mother tree) and 317 Swedish derived seedlings (4–20 half-sibs per mother tree). The descriptors used for this ex situ morphological characterization are given in Table 2. In 1995, three of these descriptors, viz. growth, canker susceptibility owing to *Pseudomonas* spp., and fruit colour, were recorded, while growth was the only character not recorded in 1997. Fruit and stone weight were recorded in sets of 50 fruits, while length of stem peduncle was measured on 20 samples.

2.3. Statistical analysis

Analyses of variance (ANOVA) and principal component analyses were carried out in all data sets with the aid of MSTAT-C (Anonymous, 1989). If offsprings from each mother tree are progeny tested, the resultant variation can be

Table 2
Descriptors considered for the ex situ morphological variation between 28 half-sib populations from Denmark and Sweden

Descriptor	Scale
Growth	1 = weak, 9 = vigorous
Stem number	Count
Canker	1 = resistant, 9 = susceptible
Intensity of bloom	1 = none, 9 = best
White buds	Percentage in flower development between green clusters and full bloom
Full bloom	Percentage (=100 – percentage white buds)
Fruit set	1 = low, 9 = best
Fruit colour	1 = yellow, 4 = red, 6 = black
Maturity	1 = early, 2 = medium, 3 = late
Fruit shape	2 = flat round, 3 = round, 4 = elongate
Fruit weight	g
Fruit peduncle	mm
Weight 100 stones	g

partitioned into within and between maternal groups (Hill et al., 1998). Therefore, the percentage accounted for by the sum of squares owing to the half-sib population was calculated in the ex situ data. This half-sib analysis provides indirect information about the amount of additive genetic variation (V_A) in the reference material because the covariance between half-sibs is equal to 1/4 V_A. Thus, information regarding narrow-sense heritability (h^2) of a characteristic may be obtained because $h^2 = V_A/V_P$, where V_P is the total phenotypic variation. Heritability has been used by plant breeders to calculate gains from selection; the higher the heritability, the greater the expected gain from selection.

Principal component analysis (PCA) is a method which can be used to identify patterns in a set of biological data derived from recording several characteristics at a time (Iezzoni and Pritts, 1991). The analysis transforms the original correlated measurements into uncorrelated linear combinations of these variables (Hill et al., 1998). PCA explains the variance/covariance structure of the data set with a few (usually 2) linear combinations of the original variables. Each combination consists of a set of weightings known as principal components (PRINs), which are functions of the eigenvalues (λ_i) and eigenvectors (e_i) of the variance/covariance matrix of the original data. The latent roots determine the number of the most important characteristics loading the PRINs, and these characteristics are those with the highest e_i. A descriptor by accession matrix was generated for this PCA and latent vectors were derived from the correlation matrix. First and second principal components (PRIN 1 and PRIN 2, respectively) were plotted to enhance the dispersion of the accessions, based on the respective list of descriptors. Successive components (PRIN 3 onwards) accounted for a decreasing proportion of the total variation and were not included in the graphs.

3. Results

3.1. In situ assessment

On average, there were significant differences ($P < 0.05$) among the three Scandinavian states for height, habitus 2, fruit size, fruit taste and flesh colour (Table 3). The tallest and most erect trees were those of Norway. Swedish cherries were larger and more tasty than those from the neighbouring countries. The flesh colour was darker in Norway than in Sweden. Furthermore, the characteristics recorded in Bornholm were similar between populations, while height, fruit set, colour and taste varied significantly among the two Norwegian populations. Likewise, height, habitus 1, fruit set, size and colour, and stone size were significantly different among Swedish populations. It seems that fruits become smaller in the north than in the south of Sweden (I. Fernqvist, SLU, Sweden, pers. commun.).

Table 3
Average in situ morphological and fruit variation between 36 Scandinavian populations of sweet cherry (descriptor and scale or unit indicated in Table 1)

Location	Height	Habitus 1	Habitus 2	Fruit				Flesh colour	Stone size
				Set	Size	Colour	Taste		
Denmark	9.5	1.0	2.0	3.5	10.9	4.8	3.5		
Norway	13.7	1.0	1.2	3.2	12.9	3.5	3.4	1.4	9.0
Sweden	7.6	1.1	1.9	2.9	20.2	4.5	4.0	2.6	9.3
P (F-tests)									
Between states	0.016	[a]	0.008	0.063	[b]	[a]	0.048	0.038	[a]
Within Norway	[b]	[a]	[a]	0.002	0.223	0.038	0.001	0.282	0.189
Within Denmark	[a]	[a]	[a]	[a]	0.114	0.380	0.379		
Within Sweden	[b]	0.002	0.071	[b]	[b]	0.005	0.152	0.370	[b]

[a] Indicates F-test smaller than 1.
[b] *P* (F-test) <0.001.

The first principal component (PRIN 1) accounted for 30.9% of the total variation and was unevenly loaded (Table 4). The most important loading characteristics were fruit taste and fruit size as determined by the latent vectors and latent roots. Similarly the second principal component (PRIN 2), which accounted for another 17.6% of the total variance was unevenly loaded. The most important loading characters were habitus 1 and fruit set as indicated by its eigenvector and latent root. The PCA biplot (Fig. 1) shows Swedish and Danish populations clustered together, while one of the two Norwegian populations was mixed with those from Denmark. Both Danish and Norwegian populations are placed towards the left on the PRIN 1 axis, and thus characterized by their acid

Table 4
Eigenvectors for the first, second, third, fourth and fifth principal components of the in situ data assessment of Scandinavian sweet cherry

Descriptor	PRIN 1	PRIN 2	PRIN 3	PRIN 4	PRIN 5
Height	−0.417	0.335	0.309	0.441	−0.359
Habitus 1	0.321	0.613	−0.062	−0.129	−0.569
Habitus 2	0.301	0.411	0.428	−0.466	0.428
Fruit set	−0.446	0.442	0.146	0.208	0.482
Fruit size	0.431	0.035	−0.090	0.612	0.315
Fruit colour	−0.012	0.383	−0.797	0.012	0.179
Fruit taste	0.498	0.012	0.229	0.391	−0.028
Latent roots	2.162	1.231	1.124	0.973	0.687
Percentage variance	30.891	17.587	16.061	13.905	9.807
Cumulative variance	30.891	48.478	64.539	78.444	88.251

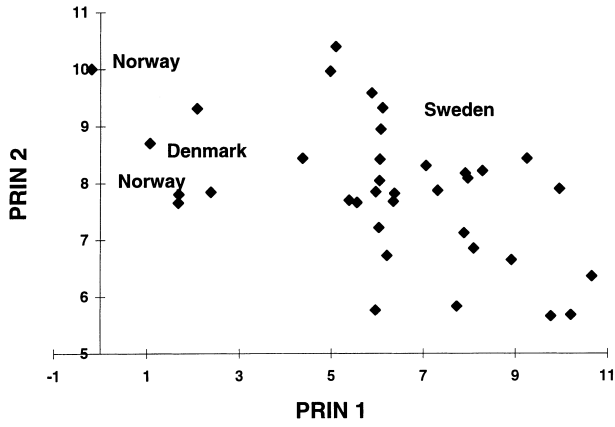

Fig. 1. Positions of principal component (PC) scores of different Scandinavian accessions of sweet cherry based on in situ assessment.

fruit taste and small fruit size. Their relatively high score on the PRIN 2 axis was explained by a specific habitus (one stem tree) and heavy fruit set. The Swedish populations exhibited the greatest variation, and their PRIN 1 score was higher than those from Danish and Norwegian populations. This result was not surprising because of the widespread distribution of sweet cherry in Sweden (about 600 km from south to north).

3.2. Ex situ assessment

The populations from Denmark had on average significantly ($P < 0.05$) larger growth, darker colour, higher host resistance to canker, but lower fruit weight and weight of 100 stones than Swedish populations (Tables 5 and 6). The other characteristics were statistically similar in open-pollinated derived populations collected either in Denmark or Sweden. Further analysis of variation for each characteristic within Denmark and Sweden showed significant ($P < 0.05$) variation within each country for most characteristics except canker resistance and maturity in Denmark, and maturity and fruit shape in Sweden.

PRIN 1 explained 39.8% of the total variation and was unevenly loaded (Table 7). The most important positive loading characteristics of PRIN 1 were growth and intensity of bloom, while the most negative loading characteristic of PRIN 1 was host resistance to canker. Similary PRIN 2, which accounted for 21% of the total variation, was unevenly loaded. The most important characteristics of PRIN 2 were fruit colour (negative) and percentage of white buds (positive). Fig. 2 shows the PCA biplot in which arrows indicate the Danish populations. In this assessment there was no clear cut distinction between Danish and Swedish populations as in the in situ assessment.

Table 5
Average ex situ morphological variation between 28 Danish and Swedish populations of sweet cherry (descriptor and scale or unit indicated in Table 2)

Population	Stem			Bloom intensity	White buds (%)	Fruit set	Fruit colour
	Growth	Number	Canker				
Denmark	6.5	2.1	3.2	6.6	23.4	2.1	5.4
Sweden	5.4	2.4	4.2	6.2	23.2	1.9	4.5
P (F-tests)							
Between states	[a]	0.188	0.035	[b]	[b]	[b]	0.008
Within Denmark	[a]	[a]	[a]	[a]	[a]	[a]	[a]
Within Sweden	0.026	0.013	[a]	[a]	[a]	[a]	0.004

[a] *P* (F-test) <0.001.
[b] Indicates F-test smaller than 1.

Table 6
Average ex situ fruit variation between 28 Danish and Swedish half-sib populations of sweet cherry (descriptor and scale or unit indicated in Table 2)

Population	Maturity	Fruit			Weight of 100 stones
		Shape	Weight	Peduncle	
Denmark	2.0	3.8	1.3	39.3	147
Sweden	2.2	3.8	1.7	39.4	182
P (F-tests)					
Between states	0.121	[a]	0.006	[a]	0.002
Within Denmark	[a]	0.022	0.006	0.003	[b]
Within Sweden	0.088	0.439	0.012	0.002	0.004

[a] Indicates F-test smaller than 1.
[b] *P*(F-test) < 0.001.

Table 7
Eigenvectors for the first, second, third, fourth and fifth principal components of the ex situ data assessment of Swedish and Danish sweet cherry

Descriptor	PRIN 1	PRIN 2	PRIN 3	PRIN 4	PRIN 5
Growth	0.441	−0.032	0.564	0.033	−0.037
Fruit colour	0.309	−0.598	0.220	0.030	0.588
Canker	−0.515	0.020	−0.138	−0.189	0.666
Intensity of bloom	0.428	0.274	−0.468	0.021	0.175
Percentage of bloom	−0.041	0.570	0.520	−0.472	0.180
Number of stems	−0.291	0.229	0.296	0.831	0.135
Fruit set	0.418	0.435	−0.192	0.220	0.358
Latent roots	2.787	1.474	1.085	0.826	0.356
Percentage variance	39.814	21.052	15.501	11.807	5.088
Cumulative variance	39.814	60.866	76.367	88.173	93.261

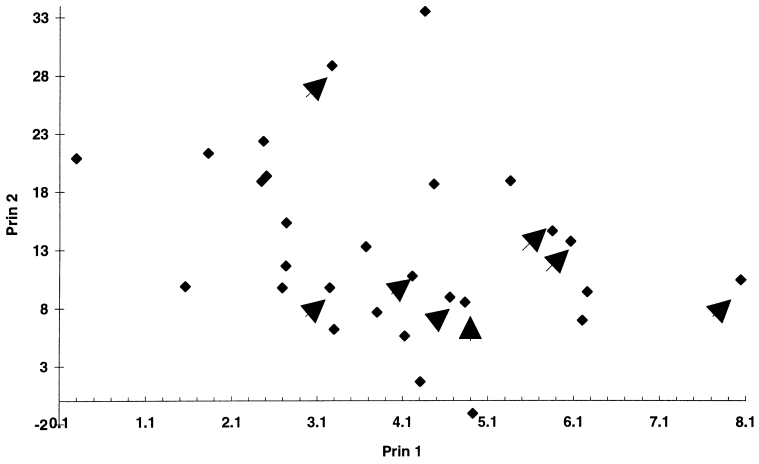

Fig. 2. Positions of principal component (PC) scores of different Swedish and Danish (indicated with arrows) accessions of sweet cherry based on ex situ assessment.

Table 8
Percentage of the total variation of ex situ assessment of Swedish and Danish sweet cherry accounted for by the variation among open-pollinated half-sib (HS) populations

Characteristic	HS from Denmark	HS from Sweden
Growth	17.6	9.9
Fruit colour[a]	28.0	32.0
1995	46.2	52.1
1997	18.0	33.2
Canker[a]	8.0	16.7
1995	20.0	64.3
1997	27.9	64.2
Intensity of bloom	31.6	30.5
Percentage of white buds	24.5	28.8
Percentage of full bloom	24.0	28.1
Stem number	8.9	10.8
Fruit set	35.4	56.0
Maturity	10.2	25.6
Fruit shape	19.9	15.7
Fruit weight	17.9	29.2
Fruit peduncle	22.5	35.0
Weight of 100 stones	30.7	31.4
Open-pollinated half-sibs	300	317
Mother trees of HS	8	20
Locations where mother trees were grown	3	7

[a] Combined over years.

The percentage of sum of squares (SS) of the analysis of variance accounted by the variation among the open-pollinated half-sibs (HS) was calculated for each descriptor (Table 8). The results suggest an intermediate to high heritability for intensity of bloom, fruit set, fruit colour, fruit peduncle and stone weight. For the two characteristics recorded in 1995 and 1997 (fruit colour and resistance to canker), the percentage of SS due to HS populations in the combined ANOVA was lower than those from the individual ANOVA. Both the environment (i.e., date of data recording) and the genotype-by-environment interaction significantly ($P < 0.001$) affected fruit colour and host resistance to canker. Therefore, heritability calculated in single environments (one date for recording or only one location) may be biased upwards, which explains the conflicting results from the individual and combined ANOVAs for fruit colour and host resistance to canker.

4. Discussion

Sweet cherry is a species with great phenological and morphological variation. In addition it has a wide natural distribution, thereby ecotypes are expected to develop. The pattern of spatial relationship obtained for Scandinavian populations based on the in situ assessment suggests distinct ecotypes of sweet cherry within Scandinavia. Kolesnikova (1975) (cited by Iezzoni et al., 1990) listed five ecotypes of sweet cherry in the former USSR. This division was based on differences in winter hardiness and fruit quality. In our investigation fruit quality (i.e., fruit taste and size) and fruit set were important factors for clustering, which agreed with the Kolesnikova's findings because good fruit set can only be achieved if trees are hardy enough. Distinct ecotypes are not unique to sweet cherry, for example ecotype differentiation occurs in red currant (*Ribes rubrum*), another fruit species native to Scandinavia (Erstad, 1996).

In the ex situ assessment of this investigation, clustering according to geographical origin was not obtained among the open pollinated half-sibs. This discrepancy could be explained by the influence of the environment, the genotype-by-environment interaction, the populations whose seeds were chosen for deriving seedlings, and the descriptors used for the in situ or ex situ research. Indeed, phenotypic variation determined by in situ assessments may not be always true, while the phenotypic variation ascertained by ex situ assessments may be confounded by the genotype-by-environment interaction, or could depend on the new genotypes arising from seed propagation after open-pollination.

The percentage of total variation for fruit colour accounted for by the half-sib populations was on average 30%, thereby suggesting an intermediate h^2 for this characteristic. Fruit colour seems to be controlled by one gene, and with "dark" colour being dominant over "light" colour (Theiler-Hedtrich, 1985a). The other fruit characteristic which also seems to have an intermediate h^2 was fruit

peduncle, which has been reported to be simply inherited, and with short length dominant over long (Brown et al., 1996). The characteristic intensity of bloom, whose variation among half-sib populations accounted in excess of 30%, has a complex inheritance and the phenotypes for this characteristic may depend on different factors such as hardiness. Fruit set has been reported to be a recessive characteristic because only 5–20% of seedlings obtained were high yielding even if the parental plants were both very good croppers (Theiler-Hedtrich, 1994). In our experiment, this characteristic appears to have the highest h^2 as determined by the percentage of sum of squares accounted by the variation among half-sibs. The inheritance to bacterial canker resistance in seedlings was investigated by Theiler-Hedtrich (1985b), who suggested that resistance to this disease was under polygenic control. Such a polygenic system may be affected by the environment and the genotype-by-environment interaction as suggested by our results.

Vittrup Christensen (1970) investigated what sweet cherry descriptors could serve to differentiate between cultivars. This researcher reported that fruit size and fruit peduncle may be among the most important descriptors for such an assessment. Juice colour was another characteristic suggested by Vittrup Christensen (1970) as a cultivar descriptor to discriminate between coloured and uncoloured fruits. Skin fruit colour has been considered to be influenced by climatic conditions, which could affect the ex situ assessment in our study. Time of ripening has been suggested as a good cultivar descriptor because known cultivars of sweet cherry ripen over a seven week period. Consequently, our single rating of maturity on a 1–3 scale could not have been precise enough. Perhaps to obtain an accurate assessment of phenotypic variation in sweet cherry it is necessary to study populations over a long period.

Ideally, clones should be propagated and planted in the same testing field and perhaps near the location where the gene bank curator works. Propagation should be either through grafting on the same rootstock cultivar or by micropropagation. Such a procedure provides a means for sequential observations of the clonally propagated germplasm over a long period, thereby supplying reliable data for statistical analysis. Molecular or biochemical characterization may be an alternative for description of wild and cultivated sweet cherry germplasm (Gerlach and Stösser, 1997; Beaver et al., 1995). For example, Fernqvist and Huntrieser (1988) used wild sweet cherry as a model for isoenzyme analysis of fruit cultivars and genotypes. Six enzyme systems were enough to identify distinct Scandinavian genotypes. Similarly, Italian populations of wild sweet cherry were investigated with seven isoenzyme systems (Ducci and Proietti, 1997). The intrapopulation variability was highest in the northern part of Italy, where these populations were situated close to one another, while the between population variation was high in areas with sparse distribution. Stylar ribonucleases have also been studied to determine incompatibility within cultivars and progenies of sweet cherry (Boskcovic and Tobutt, 1996; Boskcovic et al., 1997).

Kleinschmit and Stephan (1998) have suggested in situ conservation of natural stands with a minimum of 30–50 individual trees, and ex situ conservation in regional seed orchards. In addition to field gene banks, cryopreservation has also been recommended as a back-up conservation system of genetic resources of *Prunus* (Gass et al., 1996). A thorough assessment of wild sweet cherry germplasm will help to obtain clonal archives comprising most of the variability of horticulturally important characteristics. Hence, important characteristics for fruit producers, such as host resistance to canker and cracking, self-fertility, dwarfing, seed germination, and tree size uniformity, should be considered by gene bank curators in their assessment of variation among sweet cherry accessions.

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