Inbreeding, Coancestry, and Founding Clones of Almonds of California, Mediterranean Shores, and Russia

Ali Lansari

Ecole Nationale d'Agriculture, B.P. S/40, Meknes, Morocco

Dale E. Kester

Department of Pomology, University of California, Davis, CA 95616

Amy F. Iezzoni

Department of Horticulture, Michigan State University, East Lansing, MI 48824

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Abstract. The mean inbreeding and coancestry coefficients were calculated for almond, *Prunus dulcis* (Miller) D.A. Webb, cultivars from the United States, France, Spain, Israel, and Russia. To improve cultivars to meet market demand, the recurrent use of four selections as parents in U.S. breeding programs has resulted in a mean inbreeding coefficient (F) of 0.022 in this collection. In France, a single cultivar, Ferralisse, has an inbreeding value of $F = 0.250$, while cultivars of other almond-producing countries are noninbred ($F = 0$). Due to the use of common parents, U.S., Russian, and Israeli cultivars share coancestry, while coancestries also exist between French and Spanish almond germplasm. Cultivars of known parentage in the United States, Russia, Israel, France, and Spain trace back, respectively, to nine, eight, three, four, and three founding clones. Future almond-breeding programs may narrow the genetic base and thereby limit genetic gain.

Genetic diversity of crop plants decreases the likelihood of epidemic crop losses to insects, diseases, and unfavorable stress conditions. Maximizing genetic diversity is also important in breeding programs, since it enhances the potential gain from selection. Yet *Prunus* cultivars grown in the United States have a very narrow genetic base. Sour cherry (*P. cerasus* L.) production in the United States is a monoculture of one cultivar, and most commercial peach [*P. persica* (L.) Batsch.] cultivars trace back to six parental cultivars (Scorza et al., 1985). In almond (*P. dulcis* synonymous *P. amygdalus* Batsch) breeding programs, the extensive use of a few cultivars as parents suggests that the almond germplasm base may also be similarly narrow (Kester et al., 1991).

The cultivated almond is believed to have originated from the wild species *Amygdalus communis* L. (Evreinoff, 1958; Grasselly and Crossa-Raynaud, 1980; Kester, 1990; Kester et al., 1991; Kester and Asay, 1975). *A. communis* is thought to be derived from hybridization among several wild species of the subgenus *Amygdalus* such as *P. fenziiana*, *P. bucharica* (Grasselly and Crossa-Raynaud, 1980; Kester and Asay, 1975), *P. ulmifolia* (Evreinoff, 1958; Kester and Asay, 1975), and possibly *P. kuramica* (Grasselly and Crossa-Raynaud, 1980; Kester et al., 1991), and *P. kotschii* (C. Grasselly, personal communication). Native habitats of the cultivated almond are between 700 and 1700 m on the Kapet Dag Mountains between Iran and Russia and on the Tian Shan Mountains between western Mongolia and Russia (Grasselly, 1976; Grasselly and Crossa-Raynaud, 1980; Kester, 1990; Kester and Asay, 1975). Almond cultivation began during the 3rd millennium B.C. (Socias i Company, 1990) with sweetkerneled selections that arose by mutation in wild populations of normally bitter

seedlings (Grasselly, 1976; Kester, 1990). Cultivated almonds were introduced to Greece before 350 B.C. (Kester, 1990; Socias i Company, 1990) and spread around the Mediterranean through commercial routes (Grasselly and Crossa-Raynaud, 1980; Kester, 1990; Kester et al., 1991; Kester and Asay, 1975; Socias i Company, 1990). The Arabs introduced almonds into North Africa and the Iberian peninsula during the 6th and 7th century A.D. (Kester, 1990). The introduction of almonds into America, Australia, and South Africa occurred between 1850 and 1900 (Kester, 1990). Currently almond culture is concentrated in three world regions: Asia, the shores of the Mediterranean Sea, and California. Limited production occurs in Australia, South Africa, Argentina, and Chile (Kester et al., 1991).

Since antiquity, the cultivated almond has been propagated both by seeds and as clones and, therefore, may have undergone more selection pressure than a predominantly clonally propagated species. As a result of this selection pressure, the domesticated species progressively differentiated into separate geographical ecotypes in differing environments (Grasselly, 1976; Grasselly and Crossa-Raynaud, 1980; Kester, 1990). Cultivars were selected from seedling almond populations, grafted to propagate desirable clones, and later established in commercial orchards (Kester, 1990; Kester et al., 1991; Kester and Asay, 1975; Socias i Company, 1990). Most of the leading cultivars originated from chance seedlings selected from local gene pools (Kester et al., 1991).

Almond production and cultivar development has followed different patterns in different parts of the world: 1) Seedlings and a few locally selected and vegetatively propagated cultivars are grown commercially in Afghanistan, Bulgaria, India, Iraq, Iran, Morocco, Pakistan, Romania, Syria, Turkey, and the former Yugoslavia. 2) Breeding and evaluation programs exist in Australia, Greece, Israel, Italy, Spain, Tunisia, and the United States, but most of their major cultivars originated from chance seedlings from local ecotypes. 3) In France and Russia, the almond industries rely primarily on cultivars released from breeding programs, while old seedling or clonally selected cultivars from landraces now exist only in germplasm collections. Almond is an obligate outcrosser

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and susceptible to inbreeding depression characterized by low vigor and reduced flower number, fruit set, seed germination, seedling survival, leaf abnormalities, and disease resistance (Grasselly and Olivier, 1976, 1981; Grasselly et al., 1981; Socias i Company, 1990). When the 'Tuono' cultivar from the Puglia region of Italy was crossed with unrelated cultivars, no inbreeding depression was reported. However, when 'Tuono' was crossed with other cultivars from the same region and self-pollinated, inbreeding depression was observed as low vigor and a longer juvenile period (Socias i Company, 1990). In breeding programs, when self-pollination or sib-mating is practiced, the level of inbreeding in the progeny increases. The objective of self-pollinations or related crosses is generally to maintain the uniformity in kernel traits required by the industry. As a result, there is fixation at desirable loci with an associated reduction of fitness due to a loss of heterozygosity. The extensive use of related parents in almond breeding programs raises a concern of possible inbreeding depression. The objective of the present study was to compare the level of inbreeding, coancestry, and the genetic contribution of founding clones among almond germplasm in selected almond-producing countries.

Materials and Methods

Pedigrees of almond cultivars were collected from breeding records and published sources (Anonymous, 1977; Asai et al., 1994; Barbera et al., 1984; Bastide and Souty, 1976; Brooks and Olmo, 1972, 1982; Chessa and Pala, 1985; Costetchi, 1967; Egea et al., 1984; Fanelli, 1939; Felipe, 1976, 1984; Felipe and Socias i Company, 1985, 1987; Georgio et al., 1985; Grasselly and Crossa-Raynaud, 1980; Jaouani, 1976; Kester et al., 1984, 1991; Monastral et al., 1984; Serafimov, 1976; Spiegel-Roy, 1976; Spiegel-Roy and Kochba, 1976a, 1976b; Spiegel-Roy et al., 1982; Stylianides, 1976, 1977; Vargas Garcia, 1975; Vlasic, 1976; Wood, 1924). Parental relationships for many cultivars of unknown origin have been determined by isozyme techniques (Hauagge et al., 1987), or through pollen incompatibility studies (Asai et al., 1994; Crossa-Raynaud and Grasselly, 1985; Godini et al., 1977). Pedigrees for 123 almond cultivars were obtained, of which 85 were American, 12 Russian, 6 Israeli, 12 French, 5 Spanish, and 3 Italian (Table 1). 'Princesse' used in the United States and Russian breeding programs was considered the same in our analysis since both the Russian and U.S. 'Princesse' trace back to the same French papershell germplasm. However, the U.S. and Russian 'Princesse' may represent different clonal selections (Ch. Grasselly, personal communication).

The inbreeding coefficient (F), given by the following formula, is defined as the probability that two genes at any locus in an individual are replicates of one and the same gene in a previous generation. These genes are said to be "identical by descent" (Wright, 1922).

$$F_x = \sum \left[\left(\frac{1}{2} \right)^{n_1 + n_2 + 1} (1 + F_A) \right]$$

where n_1 = number of generations from one parent back to the common ancestor, n_2 = number of generations from the other parent back to the common ancestor, and F_A = inbreeding coefficient of the common ancestor.

Estimation of the level of inbreeding by calculation of the inbreeding coefficient gives a reasonable approximation of the probability of gene fixation, even when the initial gene frequencies are not known (Wright, 1922). Considering that almond is an obligate outcrosser because it is self-incompatible, all parents of unknown origin were assumed non-inbred and unrelated. The seed

Table 1. Almond cultivars from the U.S., Russia, France, Israel, Spain, and Italy.

	<i>United States</i>	
Arbuckle	I.X.L.	Profuse
Bigelow	Janice	Reinero
Bonita	Jeffries	Ripon
Ballico	JordanoloRoy	Roy
Bell	Jubilee	Ruby
Burbank	Kapareil	Robson
Butte	Kern Royal	Sans Faute
Carmel	Kutsch	Sonora
Craven	Livingston	Solano
Carrion	La Marie	Sydney Special
Cressey	La Prima	Smith X.L
Davey	Leweling	Standard
Drake	Legrand	Spencer
Dehn	Merced	Sauret #1
Emerald	Milow	Sauret #2
Empire	Mission (Texas)	Swanson
Elsie	Monterey	Tardy Nonpareil
Eureka	Moneytree	Thompson
Fritz	Monarch	Tioga
Golden Street	Norman	Tokyo
Godde	Nonpareil	Titan
Granada	Ne Plus Ultra	Utah
Grace	Northland	Valenta
Heart	Pioneer	Vesta
Hoover	Planada	Walton
Hallshardy	Padre	Wawona
Harpareil	Peerless	Yosemite
Harriott	Paxman	
Harvey	Price Cluster	
	<i>Russia</i>	
Bumagnoskorlupii	Nikitski 62	Primorski
Desertnyi	Nikitski 1	Prenii
Krimski	Nikitski 53	Sovietski
Miagkoskorlupii	N.Pozdentvetusei	Yaltinski
	<i>France</i>	
Ai	Ferragnes	Lauranne
Ardechoise	Ferraduel	Princesse
Belle d'Aurons	Ferrastar	Stelliette
Ferralise	Lanugedoc	Tardive de la Verdrière
	<i>Israel</i>	
Dagan	Poriah 10	Samish
Greek	Solo	Kochba
	<i>Spain</i>	
A-10-6	Jordan	Marcona
Ayles	Moncayo	
	<i>Italy</i>	
Cristomorto	Reams	Tuono

parent involved in an open-pollination was also assumed to be unrelated to the pollen parent. Inbreeding coefficients were calculated using a computer program of Hancock and Siefker (1982).

The coancestry coefficient (CC) of prospective progeny of two individuals is equal to one half the covariance of the parents. Since F of an individual is equal to the CC of its parents, the CC of two cultivars was calculated as F of their prospective progeny. Common CC are 0.500 for self-pollination, 0.250 for parent-offspring and full-sib matings, 0.125 for half-sib matings, and 0.063 for first-cousin matings. Parentage of a mutant of a cultivar is considered

to be the same as parentage of the mutated cultivar. Thus only the CC value of the original cultivar is presented. However, the CC values of all the cultivars (Table 1), the mutants plus the original cultivar, were considered for mean calculations.

The genetic contribution (GC) of a founding clone to a cultivar was calculated as described by Sjulín and Dale (1987):

$$GC = \sum_{i=1}^x \left(\frac{1}{2}\right)^n$$

where n = number of generations in a pedigree pathway between the founding clone and the cultivar, and x = number of pathways between the founding clone and the cultivar.

Results

Inbreeding coefficients. Only 10 of the 123 almond cultivars analyzed had an inbreeding coefficient other than zero (Table 2). U.S. cultivars ranged from F = 0 to 0.375 with 9 of the 85 cultivars having F > 0 (Table 2). The mean for the U.S. cultivars was F = 0.022. Except for the French cultivar 'Ferralise', with F = 0.250, all the remaining almond cultivars in France, Russia, Spain, and Israel are noninbred (F = 0).

Founding clones. The U.S. almond cultivars trace back to nine cultivars, with 'Nonpareil', 'Mission', and the French 'Princesse' and 'Languedoc' representing the highest genetic contribution (GC) (Table 3). 'Nonpareil', a seedling of 'Princesse', contributes 37.9% of the genetic composition of U.S. cultivars. This cultivar is related to 65% of the cultivars studied. 'Mission' (Syn. 'Texas') has a GC of 30.2% and a coancestry relationship with 49% of the cultivars under study. 'Princesse' has a GC of 21.6%, while 'Languedoc' has a GC of 14.1%. The gene pool in California is dominated by descendants of 'Nonpareil' and 'Mission' (Hauagge et al., 1987; Kester et al., 1991). 'Nonpareil', 'Ne Plus Ultra', 'I.X.L.', and 'Mission' are considered founding clones because of their extensive use (mostly 'Mission' and 'Nonpareil') in breeding programs. In addition, they originated from the first generation of selected almonds. The maternal parent of 'Nonpareil' (as well as 'Ne Plus Ultra' and 'I.X.L.') is believed to be a variety known in

California as 'Princesse', which originated in the Languedoc area of France (Grasselly and Crossa-Raynaud, 1980). 'Languedoc', also known as 'Princes', was also introduced from the Languedoc area of France (Kester et al., 1991).

The Russian cultivars trace back to eight founding clones (Table 3). Three of the founding clones are of Russian origin ('Nikitski 62', 'Nikitski 1', and 'Nikitski 53'), while the other five are from France ('Princesse' and 'Languedoc'), Italy ('Fragullio' and 'Reams'), and the United States ('Nonpareil'). The dominant cultivar used in Russian breeding programs is 'Nikitski 62' (GC = 38.9%), followed by 'Princesse' (GC = 16.7%). 'Nikitski 1', 'Languedoc', and 'Nonpareil' have a GC of 11.1%.

The French almond-breeding program is characterized by the extensive use of four founding clones: 'Ai' (France) (GC = 35.7%), 'Cristomorto' (Italy) (GC = 35.7%), 'Tuono' (Italy) (GC = 14.3%), and 'Ardechoise' (France) (GC = 7.1%) (Table 3). All other French almond cultivars are of a chance seedling origin with unknown parentage except some speculative parentage relationship between old cultivars such as 'Fourcouronne', 'Tournafort', and 'Tardive de la Verdrière' (Grasselly and Crossa-Raynaud, 1980).

The cultivars released from the Spanish breeding program are

Table 3. The percent genetic contribution of founding clones in all cultivars in the respective country of origin.

Founding clone	Country of origin	Genetic contribution within each country (%)
<i>American</i>		
Nonpareil	United States	37.9
Mission	United States	30.2
Princesse	France	21.6
Languedoc	France	14.1
I.X.L.	United States	3.9
Eureka	United States	2.3
Harriott	United States	1.6
Ne Plus Ultra	United States	1.3
Swanson	United States	0.7
<i>Russian</i>		
Nikitski 62	Russia	38.9
Princesse	France	16.7
Nikitski 1	Russia	11.1
Nonpareil	United States	11.1
Languedoc	France	11.1
Nikitski 53	Russia	5.6
Fragullio	Italy	5.6
Reams	Italy	5.6
<i>French</i>		
Cristomorto	Italy	41.7
Ai	France	33.3
Tuono	Italy	16.7
Ardechoise	France	8.3
<i>Spanish</i>		
Tuono	Italy	50.0
Ferragnes	France	16.7
Tardive	France	16.7
<i>Israeli</i>		
Greek	Israel	25.0
Marcona	Spain	25.0
Princesse	France	25.0

Table 2. Country of origin, parentage, and inbreeding coefficients for 10 almond cultivars.

Country of origin	Cultivar	Presumed or reported parentage	Inbreeding coefficient (F)
U.S.	Sonora (5a-20)	21-19W [Nonpareil x (Nonpareil x Eureka) A1-30] x 22-20 [Nonpareil x (Nonpareil x Eureka) A1-30]	0.375
U.S.	Solano (5a-3)	21-19W [Nonpareil x (Nonpareil x Eureka) A1-30] x 22-20 [Nonpareil x (Nonpareil x Eureka) A1-30]	0.375
U.S.	Emerald	Mission x (Nonpareil x Mission)	0.250
U.S.	Profuse	Nonpareil x Jordanolo	0.250
U.S.	Wawona	Ruby x Mission	0.250
U.S.	Kapareil	Nonpareil x 24-6[Sel. A525 (Nonpareil x Eureka) x Eureka]	0.125
U.S.	Milow	Nonpareil x 24-6[Sel. A525 (Nonpareil x Eureka) x Eureka]	0.125
U.S.	Vesta	Solano (5a-3) x late blooming sport of Nonpareil	0.094
U.S.	Davey	Nonpareil x Sans Faute	0.063
France	Ferralise	Ferraduel x Ferragnes	0.250

Table 4. Coefficients of coancestry for U.S. almond cultivars.^z

Cultivars	1 ^y	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 Arbuckle ^w	250 ^v	125	125	016	250	125	125	063	156	125	--- ^u	063	125	156	125	125	250	125
2 Ballico			---	---	188	125	125	125	125	---	---	---	---	---	---	125	250	---
3 Davey				047	070	---	---	---	094	140	---	188	141	176	141	---	---	176
4 Dehn					008	---	---	---	063	016	---	125	016	020	016	---	---	020
5 Emerauld						188	188	094	203	063	---	031	063	078	063	188	375	078
6 Empire							125	063	125	---	---	---	---	---	---	125	250	---
7 Fritz								063	125	---	---	---	---	---	---	125	250	---
8 Golden Street									063	---	---	---	---	---	---	250	125	---
9 Granada										031	---	250	031	039	031	125	250	039
10 Harpareil											250	063	250	156	125	---	---	156
11 Harriott												---	250	---	---	---	---	---
12 I.X.L													063	078	063	---	---	078
13 Jordanolo														156	125	---	---	156
14 Kapareil															156	---	---	344
15 Kutsch																---	---	156
16 Languedoc (F) ⁱ																	250	---
17 Mission																		---
18 Milow																		
19 Moneytree																		
20 Monarch																		
21 Nonpareil ^s																		
22 Ne Plus Ultra																		
23 Northland																		
24 Padre																		
25 Reinero																		
26 Profuse																		
27 Sans Faute																		
28 Sydney Special																		
29 Sonora																		
30 Solano																		
31 Spencer																		
32 Utah																		
33 Vesta																		
34 Wawona																		
35 Swanson																		
36 Ureka																		
37 Princesse (F)																		

^zCultivars with mean CC = 0 were not included.^yNumbers across top of table refer to cultivar numbers at far left of table.^xMean coefficients of coancestry calculated with dashes = 0.^wRepresents all 'Nonpareil' x 'Mission' offspring.^vCC values are $\times 10^3$.^uDashes indicate no inbreeding of known parents.ⁱ(F) = cultivar originated from France.^sMutations of 'Nonpareil', considered as 'Nonpareil', were not included in the table.

from three founding clones: 'Tuono' from Italy (GC = 50%), 'Ferragnes', and 'Tardive de la Verdière' from France (GC = 16.7%) (Table 3).

In Israel, the six cultivars grown are of Israeli origin. Four of them have been obtained through breeding programs involving three founding clones from three countries ('Greek' from Israel, 'Marcona' from Spain, and 'Princesse' originally from France but probably imported from the United States). The GC of each of these cultivars is 25% (Table 3).

Coefficients of coancestries. Even though several almond cultivars have inbreeding coefficients greater than zero, cultivars released from breeding programs show important coancestry relationships through the repeated use of a few superior parents.

U.S. germplasm. Coefficients of coancestries (CC) of cultivars

in the U.S. germplasm range between 0 and 0.5 (Table 4). The average CC values for individual cultivars paired with all other cultivars range between 0 and 0.15 with an overall mean of 0.080 for the 85 cultivars. Except for 12 cultivars of unknown origin and 'Nonpareil' and 'Mission', which are unrelated, all of the remaining 71 cultivars (84%) are interrelated. Seven percent of the cultivars represent a parent-offspring relationship (CC = 0.25), while 2% are full sibs. Fourteen percent represent a half-sib relationship (CC = 0.125) and 4% have CC = 0.063 (first-cousin relationship). On the average, every cultivar is related to 38 other cultivars with a range between 1 ('Swanson' founding clone) and 69 (all 'Nonpareil' x 'Mission' hybrids).

Russian germplasm. The twelve Russian cultivars and five foreign cultivars ('Princesse', 'Reams', 'Fragillio', 'Languedoc',

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	Mean ^x
	125	125	250	063	031	125	125	188	031	031	188	188	125	031	125	203	---	---	125	147
	---	125	---	---	---	125	---	---	---	---	---	---	---	---	---	188	---	---	---	069
	140	---	281	094	094	---	141	211	281	094	211	211	140	094	153	023	---	---	188	063
	016	---	031	031	250	---	016	023	063	063	023	023	016	063	025	008	---	---	063	012
	063	188	125	031	016	188	063	094	016	016	094	094	063	016	063	289	---	---	063	136
	---	125	---	---	---	125	---	---	---	---	---	---	---	---	---	188	---	---	---	065
	---	125	---	---	---	125	---	---	---	---	---	---	---	---	---	188	---	---	---	068
	---	063	---	---	---	063	---	---	---	---	---	---	---	---	---	094	---	---	---	037
	031	125	063	063	125	125	031	047	125	125	047	047	031	125	065	203	---	---	125	096
	125	---	250	063	031	---	125	250	031	031	188	188	125	031	125	016	---	---	125	062
	---	---	---	---	---	---	---	125	---	---	---	---	---	---	---	---	---	---	---	008
	063	---	125	125	250	---	063	094	250	250	094	094	063	250	109	031	---	---	250	060
	125	---	250	063	031	---	125	375	031	031	188	188	125	031	125	016	---	---	125	064
	156	---	313	078	039	---	156	234	039	039	281	281	156	039	180	020	---	188	156	104
	125	---	250	063	031	---	125	188	031	031	188	188	125	031	125	016	---	---	125	078
	---	125	---	---	---	125	---	---	---	---	---	---	---	---	---	188	---	---	---	068
	---	250	---	---	---	250	---	---	---	---	---	---	---	---	---	375	---	---	---	129
	156	---	313	078	039	---	156	234	039	039	281	281	156	039	148	020	---	188	156	104
		---	250	063	031	---	125	188	031	031	188	188	125	031	125	016	---	---	125	078
			---	---	---	125	---	---	---	---	---	---	---	---	---	188	---	---	---	065
				125	063	---	250	375	063	063	375	375	250	063	250	031	---	---	250	152
					063	---	063	094	063	063	094	094	063	063	109	031	---	---	250	060
						---	031	047	125	125	047	047	031	125	055	016	---	---	125	033
							---	---	---	---	---	---	---	---	---	188	250	---	---	068
								188	031	031	188	188	125	031	125	016	---	---	125	077
									047	047	281	281	188	047	188	023	---	---	188	120
										125	047	047	031	125	055	016	---	---	125	033
											047	047	031	125	055	016	---	---	125	031
												500	188	047	297	023	---	125	188	122
													188	047	422	023	---	125	188	122
														031	125	016	---	---	125	078
															055	016	---	---	125	031
																027	---	063	219	072
																	---	---	063	109
																		---	---	003
																			---	008
																				106

and ‘Nonpareil’) used in the Russian breeding programs have CC values between 0 and 0.250. The average CC value over all the cultivars tested is 0.061. Coefficients of coancestries mean values for cultivars showing coancestry relationships and taken individually vary between 0.015 for ‘Nikitski 53’, ‘Reams’, and ‘Fragillio’, and 0.103 for ‘Nikitski 62’. Ten percent of the cultivars from the Russian breeding programs have a parent–offspring relationship (CC = 0.250) and 4% are full-sibs (CC = 0.250). Fifteen percent of these cultivars represent a half-sib relationship (CC = 0.125), and 5% are of first-cousin type coancestry (CC = 0.063). Every released cultivar from a controlled cross is related to at least seven other cultivars.

French germplasm. The mean CC among the cultivars released from French breeding programs and two foreign cultivars used as

parents (‘Cristomorto’ and ‘Tuono’) is 0.121. ‘Ferralise’ represents the highest coancestry value (CC = 0.375) with its parents ‘Ferragnes’ and ‘Ferraduel’. Every cultivar is related to at least six other cultivars. Eight percent of the cultivars have a full-sib relationship and 20% have a parent–offspring relationship (CC = 0.250). Nineteen percent are half-sibs (CC = 0.125), and 1% are first cousins (CC = 0.063).

Spanish germplasm. The overall mean CC among the three Spanish cultivars released from breeding programs (‘Moncaya’, ‘Ayles’, and ‘A–10–6’) and the three foreign cultivars used as parents in the breeding programs (‘Tardive de la Verdière’, ‘Tuono’, and ‘Ferragnes’) was 0.108. Three cultivars, ‘A–10–6’, ‘Ayles’, and ‘Moncayo’, are half-sibs (CC = 0.125). The other CCs that differ from zero are parent–offspring relationships (CC = 0.250).

Table 5. Mean of coancestry coefficients among almond cultivars from five almond-producing countries.

Country	1 ^z	2	3	4	5
1) U.S.	0.080	0.030	---	---	0.035
2) Russia		0.061	---	---	0.013
3) France			0.121	0.067	---
4) Spain				0.108	---
5) Israel					0.093

^zNumbers across top of table refer to country numbers at far left of table.

^yDashes indicate no inbreeding of the known parents.

Every released cultivar is related to at least three other cultivars.

Israeli germplasm. The six Israeli cultivars and the three foreign cultivars ('Marcona', 'Nonpareil', and 'Princess') used in the Israeli breeding programs have an overall mean CC of 0.093. Coefficients of coancestries values vary between 0 and 0.250. All CCs equalling 0.250 (31% of the cultivars studied) represent a parent-offspring relationship, with the exception of a full-sib relationship between 'Solo' and 'Samish'. Fourteen percent of the coancestry relationships are of the half-sib type (CC = 0.125). Every released cultivar is related to five or six other cultivars. Some of the original parents are introduced cultivars. 'Princesse' is a French cultivar, probably introduced from the United States, 'Nonpareil' is from the United States, and 'Marcona' is from Spain.

Coancestry relationships among cultivars from different countries. Germplasm exchange between almond breeders in different countries has resulted in common use of some cultivars as parents. When mean CCs across cultivars within countries are considered, U.S., Russian, and Israeli almond cultivars share common parentage (Table 5). The mean CC between U.S. and Russian almond cultivars is 0.030, which is less than the CC mean values in U.S. and Russian cultivars (0.080 and 0.061, respectively). This parental relationship is mainly explained by the use of 'Princesse' and 'Languedoc,' old French cultivars, in breeding programs of both countries, and from the use of 'Nonpareil' from the U.S. by Russian breeders. The mean CC between U.S. and Israel cultivars is 0.035. The French cultivar 'Princesse' and the U.S. cultivar 'Nonpareil' are found in pedigrees of cultivars from both countries. 'Princesse' and 'Nonpareil' are also the two common cultivars used by Russian and Israeli breeders, resulting in a CC of 0.013 between the two countries. In addition, there is a coancestry relationship among cultivars between Spain and France. This coancestry relationship (CC = 0.067) resulted from the common use of the Italian cultivar 'Tuono' in both breeding programs and by the use of 'Ferragnes', a French release, in Spanish breeding programs.

Discussion

The repeated use of a few founding clones and their progeny as parents in almond-breeding programs may eventually result in loss of genetic variability and a concomitant increase in inbreeding depression in future generations. This potential genetic limitation is of particular concern since new cultivars may eventually replace local seedling ecotypes. Similar situations have been reported for numerous species (Hancock and Siefker, 1982; Lyrene, 1983; Mendoza and Haynes, 1974; Reynders and Monet, 1987; Scorza et al., 1985; Sjulín and Dale, 1987).

Most cultivars presently grown are hybrids of a few unrelated parents (e.g., 'Nonpareil' and 'Mission' in the United States). The mean inbreeding coefficient for U.S. almond cultivars is lower

than that of plums (Byrne, 1989), and 4.5 to 8 times lower than that of peaches (Reynders and Monet, 1987; Scorza et al., 1985). The analyses presented herein suggest that limited inbreeding has occurred in U.S. almond germplasm to date. However, the high degree of coancestry may limit future progress and introduce undesirable traits (e.g., noninfectious bud failure). The outstanding kernel characteristics and industry importance of 'Nonpareil' led to its extensive use as a parent in breeding programs. Most often it was crossed with the late-blooming cultivar Mission (Kester et al., 1991). Aside from the extensive breeding use of Nonpareil and Mission, these two cultivars represent, respectively, 65% and 25% of commercial almond production in California (Hauagge et al., 1987). This uniformity increases the vulnerability of California almond production to yield fluctuations due to hazards such as the bud failure disorder that is frequent with 'Nonpareil' and its descendants, which represent 48% of the cultivars examined (Kester, 1970).

Almond cultivars in other countries, except the French cultivar 'Ferralise', are not inbred. They are mostly selections of chance seedlings, with a limited number of cultivars from controlled crosses. The highest number of cultivars showing inbreeding are from breeding programs that have had more cycles of selection.

The major objectives in Russian breeding programs are frost and cold resistance combined with nut quality. 'Nikitski 62', known for its late bloom and cold hardiness, is a frequent parent (Denisov, 1988; Rikhter, 1964, 1969).

In Western Europe and North Africa, the main objectives in breeding almonds are similar, i.e., late bloom and self-compatibility (Grasselly, 1984). As a result, a few common cultivars are being used extensively as parents, such as 'Tuono', 'Ferragnes', 'Ai', and 'Cristomorto'.

Almond-breeding programs in different countries are characterized by the use of a few superior genotypes as parents. Selection of outstanding individuals as new cultivars or as parents has provided substantial improvement in important commercial traits. However, the diverse almond germplasm used in several European countries is already being replaced by a few superior cultivars (Grasselly, 1984). This situation is fostered by germplasm exchange, and in the near future will probably increase coancestry relationships between released almond cultivars, and might, in the future, affect genetic gain, narrow the almond genetic base, and increase the hazard of epidemics.

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