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Founding Clones, Inbreeding, Coancestry, and Status Number of Modern Apple Cultivars

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***Abstract*. Pedigrees of apple (*Malus ×domestica* Borkh.) cultivars were used to study worldwide genetic diversity among clones used in modern apple breeding. The most frequent founding clones were 'Cox's Orange Pippin', 'Golden Delicious', 'Red Delicious', 'Jonathan', and 'McIntosh'. Coefficients of coancestry between 50 mainstream cultivars and these clones averaged 0.03, 0.12, 0.07, 0.06, and 0.02, respectively, but they were frequently as high as 0.25 with certain pairings. Among a group of 27 cultivars carrying the *Vf* gene for scab resistance, coefficients of coancestry with the five founding clones were of the same order. Although few of the cultivars sampled were substantially inbred, inbreeding could reach serious levels in their future offspring if current breeding practices are continued. The status effective number was 8 for the mainstream group and 7 for the *Vf*-carrier clones. This indicates clearly that apple breeders are operating with a population of greatly reduced genetic diversity. Careful consideration of pedigrees and increased size of the genetic base are needed in future apple breeding strategies.**

The domestic apple (*Malus ×domestica*), one of the world's most ancient and most widely cultivated temperate fruit, may have originated in western Asia from natural hybridization between several species including *M. sylvestris* Mill., *M. sieversii* Ldb., and *M. baccata* (L.) Borkh (Roach, 1985). Twenty-five species and more than 7000 cultivars have been reported in apple; however, despite this vast genetic diversity, modern commercial apple production is dominated by only a few cultivars (Way et al., 1990). This trend toward genetic uniformity in commercial apple orchards is further accentuated by the release of additional mutants of popular cultivars (Brooks and Olmo, 1991, 1994).

Most current commercial apple cultivars have been identified as chance seedlings, but these are slowly being replaced by new selections developed by private breeders or by public research agencies. Unfortunately, financial investment in apple breeding is generally decreasing (Way et al., 1990), and many breeding programs are restricted to commercial cultivar production by crossing well-known parents. Few resources are generally put into long-term population improvement. Consequently, most apple breeders are working within a population of a limited genetic base, which is likely to handicap future genetic improvement and the progress of the apple industry.

During the last 30 years, breeding objectives have mainly focused on meeting aesthetic standards established by supermarkets, but eating quality and disease resistance are now receiving greater priority. The apple breeding programs for resistance to scab (*Venturia inaequalis* Cke.) have mostly concentrated on the *Vf* gene from *M. floribunda* Sieb. clone 821. All cultivars carrying the *Vf* gene originated from a cross between two selections of *M. floribunda* 821 x 'Rome Beauty'. Since 1970, more than 38 cultivars carrying the *Vf* gene have been released commercially (Crosby et al., 1992).

This study attempts to measure genetic diversity presently use in apple breeding throughout the world. Pedigrees available in the literature were used to study the genetic contribution of five major founding clones to a sample of 77 modern apple cultivars. Coefficients of inbreeding (Malécot, 1948) and coancestry (Cruden, 1949) and status effective number (Lindgren et al., 1995) were calculated for the 77 cultivars as indicators of genetic diversity.

Materials and Methods

Pedigrees of 439 apple cultivars (total of 377) and breeding selections from around the world were collected from available literature (Brooks and Olmo, 1972, 1975, 1978, 1984, 1991, 1994; de Coster, 1986; Cripps et al., 1993; Dayton et al., 1977; Fischer and Fischer, 1993a, 1993b; Korban et al., 1990; Le Lezec and Babin, 1992; Sadamori et al., 1973; Sansavini, 1993; Smith, 1971; Tamba et al., 1992; Wang, 1990; Williams et al., 1967, 1975, 1984; Yamada et al., 1980). From this database, 77 cultivars of known parentage released since 1970 were sampled to represent a range of countries of origin (Table 1). They were classified into two groups represented by 50 mainstream cultivars and by 27 *Vf*-carrier cultivars. The degree of relationship of these 77 clones with the five frequent founding clones, 'McIntosh', 'Golden Delicious', 'Jonathan', 'Cox's Orange Pippin', and 'Red Delicious' was investigated by calculating the individual coefficient of coancestry of each of these clones with the 50 mainstream cultivars and the 27 *Vf*-carrier cultivars. Inbreeding coefficients were calculated for the 77 cultivars themselves, being the same as the coefficient of coancestry of their two parents. Coefficients of coancestry were also calculated among the 50 mainstream cultivars, among the 27 *Vf*-carrier cultivars, and among the 77 cultivars together. This formed the base for calculating the status effective number of these populations.

Inbreeding and coancestry. Inbreeding coefficient of an indi-

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Table 1. Reported parentage, country of origin, and year of commercial release of 77 modern apple cultivars.

Cultivar	Reported parentage	Origin	Year
	Mainstream group		
Akane	Jonathan x Worcester Pearmain	Japan	1970
Akita Gold	Golden Delicious x Fuji[z]	Japan	1990
Aori	Toko[z] x Richared Delicious[z]	Japan	>1970
Arlet	Golden Delicious x Idared[z]	Switzerland	1989
Burgundy	Monroe[z] x (Macoun x Antonovka)	United States	1974
Chantecler	Golden Delicious x Reinette Clochard	France	1977
Charden	Golden Delicious x Reinette Clochard	France	1971
Cloden	Golden Delicious x Reinette Clochard	France	1977
Delcorf	Jongrimes x Golden Delicious	France	1974
Delrouval	Delcorf x Akane	France	1993
Earlidel	Red Delicious x Early McIntosh[z]	Australia	1988
Elan	Golden Delicious x James Grieve	Netherlands	1989
Elstar	Golden Delicious x Ingrid Marie[z]	Netherlands	1972
Empress	Jonamac[z] x Vista Bella	United States	1988
Falstaff	James Grieve x Golden Delicious	England	1989
Feleac	Jonathan open-pollinated	Romania	1980
Fiesta	Cox's Orange Pippin x Idared[z]	England	1986
Fushuai	Early McIntosh[z] x Golden Delicious	China	1977
Generos	Frumos de Voinesti x ((Golden Pearmain x *M. kaido*) x Jonathan)	Romania	1983
Goldsmith	Granny Smith x Golden Delicious	South Africa	1975
Greensleeves	James Grieve x Golden Delicious	England	1977
Himekami	Fuji[z] x Jonathan	Japan	1985
Hokuto	Fuji[z] x Mutsu[z]	Japan	>1970
Honeycrisp	Macoun[z] x Honeygold[z]	United States	1991
Hongbaoshi	Ralls Janet x Red Delicious	China	1988
Huaguan	Golden Delicious x Fuji[z]	China	1988
Huashuai	Fuji x Starkrimson[z]	China	1988
Jinguang	Ralls Janet x Red Delicious	China	1988
Jubile (Delbart)	Golden Delicious x Lundbytorp	France	>1970
Jupiter	Cox's Orange Pippin x Starking Delicious[z]	England	1981
Karmijn	Cox's Orange Pippin x Jonathan	Netherlands	1971
Kent	Cox's Orange Pippin x Jonathan	England	1974
Kogetsu	Golden Delicious x Jonathan	Japan	1981
Korona	(Mother x Red Rome Beauty) x Scotia[z]	Canada	1987
Luxiangziao	Jinhong[z] x (Ralls Janet x Starking Delicious[v])	China	1988
Michinoku	Kitakami[z] x Tsugaru[z]	Japan	1981
Pink Lady	Golden Delicious x Lady Williams	Australia	1986
Predgornoe	London Pippin x Red Delicious	Ukrainia	1984
Qinguan	Golden Delicious x (Ralls Janet x Red Delicious)	China	1970
Rubinovoe Duki	Jonathan x Aport Alexander	Ukrainia	1989
Sansa	Gala[z] x Akane	Japan	1989
Scarlet	Akane x Starking Delicious[v]	Japan	1984
Senshu	Toko[z] x Fuji[z]	Japan	1980
Shamrock	McIntosh spur type x Starkspur Golden Delicious[u]	Canada	1986
Skifskoe	Golden Delicious x Wagener	Ukrainia	1984
Summerdel	Red Delicious x Earliblaze	Australia	1989
Sundowner	Golden Delicious x Lady Williams	Australia	1979
Suntan	Cox's Orange Pippin x Court Pendu Plat	England	1974
Vista Bella	((Melba x Sonora) x ((Williams x Starr) x USDA34) x Julyred[z]	United States	1974
Yanshanhong	Ralls Janet x Richared Delicious[v]	China	1989
	Vf-*based group*		
Baujade	Granny Smith x (Reinette du Mans x (Golden Delicious x (Golden Delicious x F2 26829-2-2[z])))	France	1988
Britegold	Sandel[z] x (Platt Melba[z] x (Jonathan x F2 26829-2-2[z]))	Canada	1980
Dayton	((Melba[z] x (Wealthy x Starr)) x (Red Rome Beauty[y] x Melba[z])) x ((Jonathan x F2 26829-2-2[z]) x ((Melba x (Wealthy x Starr)) x (Red Rome Beauty[y] x Melba[z])))	United States	1987
Delorina	Grifer x Florina	France	1993
Enterprise	McIntosh x (Starking Delicious[v] x (Golden Delicious x F2 26829-2-2[z])) sib.	United Sates	1994

Table 1. Continued.

Cultivar	Reported parentage	Origin	Year
Florina	Jonathan x (Starking Delicious[v] x (Golden Delicious x F2 26829-2-2[z]))	France	1977
Freedom	(Macoun[z] x Antonovka) x (Golden Delicious x F2 26829-2-2[z])	United States	1983
Goldrush	Golden Delicious x (Winesap open-pollinated x (Melrose[z] x (Golden Delicious x F2 26829-2-2[z])))	United States	1994
Jolana	Spartan x PRI 370/15[t]	Czechoslovakia	1985
Jonafree	((Golden Delicious x F2 26829-2-2[z]) x Jonathan) x (Gallia Beauty[y] x Red Spy[w])	United States	1979
Liberty	PRI 54-12t x Macoun[z]	United States	1979
McShay	McIntosh x (Starking Delicious[v] x (Golden Delicious x F2 26829-2-2[z]))	United States	1981
Moira	McIntosh x (Jonathan x F2 26829-2-2[z])	Canada	1978
Novamac	McIntosh x (((Melba[z] x (Wealthy x Starr)) x (Red Rome Beauty[y] x Melba[z])) x (Jonathan x F2 26829-2-2[z]))	Canada	1978
Pionier	(Verzisoare x Jonathan) x Prima	Romania	1982
Priam	Jonathan x (Golden Delicious x F2 26829-2-2[z])	France/USA	1974
Prima	(Golden Delicious x F2 26829-2-2[z]) x ((Melba[z] x (Wealthy x Starr)) x (Red Rome Beauty[y] x Melba[z]))	United States	1970
Priscilla	Starking Delicious[v] x (McIntosh x (Golden Delicious x F2 26829-2-2[z]))	United States	1972
Redfree	Raritan[z] x (((Melba[z] x (Wealthy x Starr)) x (Red Rome Beauty[y] x Melba[z])) x (Jonathan x F2 26829-2-2[z]))	United States	1981
Retina	(Cox x Oldenburg) x F3 *M. floribunda*[t]	Germany	1991
Rewena	(Cox x Oldenburg) x F3 *M. floribunda*[t]	Germany	1991
Selena	Britemac[z] x Prima	Czechoslovakia	1990
Sir Prize	Tetraploid Golden Delicious x (Golden Delicious x F2 26829-2-2[z])	United States	1972
Trent	McIntosh x (Jonathan x F2 26829-2-2[z])	Canada	1979
Vandat	Jolana x Lord Lambourne	Czechoslovakia	1990
Voinea	Frumos de Voinesti x Prima	Romania	1985
William's Pride	(((Melba x (Wealthy x Starr)) x (Red Rome Beauty[y] x Melba[z])) x (Jonathan x F2 26829-2-2[z])) x (Mollie's Delicious[z] x Julyred[z])	United States	1988

[z]‘Britemac’ = ‘Melba’ x ‘Kildare’; ‘Early McIntosh’ = ‘Yellow Transparent’ x ‘McIntosh’; F2 26829-2-2 = (‘Rome Beauty’ x *M. floribunda* 821) x (‘Rome Beauty’x *M. floribunda* 821); ‘Fuji’ = ‘Ralls Janet’ x ‘Red Delicious’; ‘Gala’ = ‘Kidd’s Orange (‘Red Delicious’ x ‘Cox Orange Pippin’) x ‘Golden Delicious’; ‘Honeygold’ = ‘Golden Delicious’ x ‘Haralson’; ‘Idared ‘= ‘Jonathan’ x ‘Wagener’; ‘Jonamac’ = ‘McIntosh’ x ‘Jonathan’; ‘Julyred’ = ((‘Petrel’ x ‘Early McIntosh’) x (‘Williams’ x ‘Starr’)); ‘Jinhong’ = ‘Golden Delisious’ x ‘Hongtaiping’; ‘Kitakami’ = (‘McIntosh’ x ‘Worcester Pearmain’) x ‘Redgold’ (‘Golden Delicious’ x ‘Richared Delicious’); ‘Macoun’= ‘McIntosh’ x ‘Jersey Black’; ‘Melba’ = ‘McIntosh ‘open-pollinated ; ‘Melrose’ = ‘Jonathan’ x ‘Red Delicious’; ‘Mollie’s Delicious’ = (‘Golden Delicious’ x ‘Edgewood’) x (‘Red Gravenstein’ x ‘Close’); ‘Monroe’ = ‘Jonathan’ x ‘Rome Beauty’; ‘Mutsu’ = ‘Golden Delicious’ x ‘Indo’; ‘Raritan’ = (‘Melba’ x ‘Sonora’) x (‘Melba’ x (‘William’x ‘Starr’)); ‘Sandel’ = ‘Red Delicious’ x ‘Sandow’; ‘Scotia’ = ‘McIntosh’ open-pollinated; ‘Spartan’ = ‘McIntoch’ x ‘Yellow Newton’; ‘Tsugaru’ = ‘Golden Delicious’ open-pollinated; ‘Toko’ = ‘Golden Delicious’ x ‘Indo’.
[y]Made equivalent to ‘Rome Beauty’; ‘Gallia Beauty’ and ‘Red Rome Beauty’ = mutations of ‘Rome Beauty’.
[x]Made equivalent to ‘Melba’; ‘Platt Melba’ = mutation of ‘Melba’.
[w]Made equivalent to ‘Northern Spy’; ‘Red Spy’ = mutation of ‘Northern Spy’.
[v]Made equivalent to ‘Red Delicious’; ‘Starking Delicious’ = mutation of ‘Red Delicious’; ‘Starkrimson’ = mutation of ‘Starking Delicious’;’Richared Delicious’ = mutation of ‘Red Delicious’.
[u]Made equivalent to ‘Golden Delicious’; ‘Starkspur Golden Delicious’ = mutation of Golden Delicious’.
[t]Incomplete parentage.

vidual was defined by Malécot (1948) as the probability that its allelic pairs were identical by descent. The inbreeding coefficient of an individual depends on the amount of common ancestry of its two parents. The degree of relationship by descent of the two parents is their coefficient of coancestry, f, which is identical with the inbreeding coefficient, F, of their progeny. Inbreeding coefficient was computed using an algorithm developed by Alspach (1976), which is very similar to that of Cruden (1949).

All parents were treated as diploid, and parents of unknown origin were assumed to be unrelated and noninbred. Apples are mostly self-incompatible, and it was assumed that cultivars without known pedigree originated from outcrossed open-pollination, underestimating possible inbreeding. All mutants were regarded as the same as the original cultivar (for example ‘Jonared’ was listed as ‘Jonathan’). Since only few genes are expected to be different between such mutants and the original, this simplification can lead to minor overestimation of inbreeding coefficients. Allelic contributions from both parents were assumed to be equal and unaltered by breeders’ selection. As it is uncertain whether apple breeders would select for or against homozygosity, the effect of this assumption on the inbreeding coefficient estimate is unknown.

Status effective number. The status effective number of a breeding population (Lindgren et al., 1995) is defined as the number of unrelated and noninbred genotypes in an ideal panmictic population that would produce progeny with the same average coefficient of inbreeding as the progeny of the genotypes of a panmictic breeding population. Self-pollination and free mating with relatives is assumed in the panmictic breeding population. Status effective number, which can be compared with the actual census number of a population, measures the genetic diversity of that population. It can be derived for any population of known pedigree through calculating the matrix of coancestries. It can never be higher than the census number, and it generally declines with time. Status number is calculated as $Ns = 0.5/f$, where Ns is

Table 2. Inbreeding coefficients and coancestry coefficients with 'Cox's Orange Pippin', 'Red Delicious', Golden Delicious', 'Jonathan', and 'MacIntosh' of 77 modern apple cultivars.

		Coefficient of coancestry with				
Cultivar	Inbreeding coefficients	Cox's Orange Pippin	Red Delicious	Golden Delicious	Jonathan	MacIntosh
		Mainstream group				
Akane	0.000	0.000	0.000	0.000	0.250	0.000
Akita Gold	0.000	0.000	0.125	0.250	0.000	0.000
Arlet	0.000	0.000	0.000	0.250	0.125	0.000
Burgundy	0.000	0.000	0.000	0.000	0.125	0.063
Chantecler	0.000	0.000	0.000	0.250	0.000	0.000
Charden	0.000	0.000	0.000	0.250	0.000	0.000
Cloden	0.000	0.000	0.000	0.250	0.000	0.000
Delcorf	0.000	0.000	0.000	0.250	0.000	0.000
Delrouval	0.000	0.000	0.000	0.125	0.125	0.000
Earlidel	0.000	0.000	0.250	0.000	0.000	0.125
Elan	0.000	0.000	0.000	0.250	0.000	0.000
Elstar[z]	0.000	0.125	0.000	0.250	0.000	0.000
Empress	0.063	0.000	0.000	0.000	0.125	0.188
Estivale	0.000	0.000	0.250	0.125	0.000	0.000
Falstaff	0.000	0.000	0.000	0.250	0.000	0.000
Feleac	0.000	0.000	0.000	0.000	0.250	0.000
Fiesta	0.000	0.250	0.000	0.000	0.125	0.000
Fushuai	0.000	0.000	0.000	0.250	0.000	0.125
Generos	0.000	0.000	0.000	0.000	0.125	0.000
Goldsmith	0.000	0.000	0.000	0.250	0.000	0.000
Greensleeves	0.000	0.000	0.000	0.250	0.000	0.000
Himekami	0.000	0.000	0.125	0.000	0.250	0.000
Hokuto	0.000	0.000	0.125	0.125	0.000	0.000
Honeycrisp	0.000	0.000	0.000	0.125	0.000	0.125
Hongbaoshi	0.000	0.000	0.250	0.000	0.000	0.000
Huaguang	0.000	0.000	0.125	0.250	0.000	0.000
Huashuai	0.250	0.000	0.375	0.000	0.000	0.000
Jinguang	0.000	0.000	0.250	0.000	0.000	0.000
Jubilee	0.000	0.000	0.000	0.250	0.000	0.000
Jupiter	0.000	0.250	0.250	0.000	0.000	0.000
Karmijn	0.000	0.250	0.000	0.000	0.250	0.000
Kent	0.000	0.250	0.000	0.000	0.250	0.000
Kogetsu	0.000	0.000	0.000	0.250	0.250	0.000
Korona	0.000	0.000	0.000	0.000	0.000	0.125
Luxiangziao	0.000	0.000	0.125	0.125	0.000	0.000
Michinojku	0.063	0.000	0.063	0.188	0.000	0.063
Pink Lady	0.000	0.000	0.000	0.250	0.000	0.000
Predgornoe	0.000	0.000	0.250	0.000	0.000	0.000
Qinguan	0.000	0.000	0.125	0.250	0.000	0.000
Rubinovoe	0.000	0.000	0.000	0.000	0.250	0.000
Sansa	0.000	0.063	0.063	0.125	0.125	0.000
Scarlet	0.000	0.000	0.250	0.000	0.125	0.000
Senshu	0.000	0.000	0.125	0.125	0.000	0.000
Shamrock	0.000	0.000	0.000	0.250	0.000	0.250
Skifskoe	0.000	0.000	0.000	0.250	0.000	0.000
Summerdel	0.000	0.000	0.250	0.000	0.000	0.000
Sundowner	0.000	0.000	0.000	0.250	0.000	0.000
Suntan	0.000	0.250	0.000	0.000	0.000	0.000
Vista Bella	0.109	0.000	0.000	0.000	0.000	0.125
Yanshanhong	0.000	0.000	0.250	0.000	0.000	0.000
Mean	0.010	0.029	0.073	0.121	0.055	0.024
		Vf-*carrier group*				
Baujade	0.000	0.000	0.000	0.094	0.000	0.000
Britegold	0.000	0.000	0.125	0.000	0.063	0.063
Dayton	0.297	0.000	0.000	0.000	0.063	0.094
Delorina	0.000	0.000	0.063	0.031	0.125	0.000

Table 2. Continued.

Cultivar	Inbreeding coefficients	Coefficient of coancestry with Cox's Orange Pippin	Red Delicious	Golden Delicious	Jonathan	MacIntosh
Enterprise	0.250	0.000	0.125	0.063	0.000	0.250
Florina	0.000	0.000	0.125	0.063	0.250	0.000
Freedom	0.000	0.000	0.000	0.125	0.000	0.063
Goldrush	0.063	0.000	0.031	0.281	0.031	0.000
Jolana[y]	0.000	0.000	0.000	0.000	0.000	0.125
Jonafree	0.066	0.000	0.031	0.094	0.156	0.000
Liberty[y]	0.000	0.000	0.000	0.000	0.000	0.125
McShay	0.000	0.000	0.125	0.063	0.000	0.250
Moira	0.000	0.000	0.000	0.000	0.125	0.250
Novamac	0.063	0.000	0.000	0.000	0.063	0.281
Pionier	0.000	0.000	0.000	0.063	0.125	0.031
Priam	0.000	0.000	0.000	0.125	0.250	0.000
Prima	0.031	0.000	0.000	0.125	0.000	0.063
Priscilla	0.000	0.000	0.250	0.063	0.000	0.125
Redfree	0.000	0.000	0.000	0.000	0.063	0.031
Retina[y]	0.000	0.125	0.000	0.000	0.000	0.000
Rewera[y]	0.000	0.125	0.000	0.000	0.000	0.000
Selena	0.063	0.000	0.000	0.063	0.000	0.094
Sir Prize	0.250	0.000	0.000	0.375	0.000	0.000
Trent	0.000	0.000	0.000	0.000	0.125	0.250
Vanda[y]	0.000	0.000	0.000	0.000	0.000	0.063
Voinea	0.000	0.000	0.000	0.063	0.000	0.031
William's Pride	0.033	0.000	0.000	0.031	0.078	0.078
Mean	0.041	0.009	0.032	0.064	0.056	0.084
Grand mean	0.021	0.022	0.058	0.101	0.055	0.045

[z]'Ingrid Marie' assumed to derived from 'Cox's Orange Pippin' open pollination.
[y]Incomplete parentage available.

the status number, and f is the average coancestry of the population (including selfing).

Results and Discussion

Founding clones. About 64% of 439 cultivars and selections studied was found to be descended from only five founding clones: 'McIntosh' (101 cultivars), 'Golden Delicious' (87 cultivars), 'Jonathan' (74 cultivars), 'Cox's Orange Pippin' (59 cultivars), and 'Red Delicious' (56 cultivars). Among these, 96 cultivars had two or more of the five founding clones in their parentage. Other frequent cultivars occurring in pedigrees included 'James Grieve', 'Rome Beauty', and 'Wealthy'.

'McIntosh' was extensively used as a parent in Canada (it is present in pedigrees of 37 of the 65 Canadian cultivars sampled), the United States (34 of 115), and eastern Europe (11 of 41), but rarely occurred in pedigrees from other countries (5 of 159). 'Golden Delicious' was found in the pedigrees of many cultivars from Pacific-Rim countries such as Japan, China, Australia, and New Zealand (26 of 47), from western Europe (18 of 50), and to a lesser extent from the United States (21 of 115). 'Jonathan' was mostly used in breeding programs in western Europe (13 of 50) and in the United States (29 of 115). 'Cox's Orange Pippin' contributed to 30 of the 62 cultivars released from the United Kingdom compared to 15 of the 50 cultivars from western Europe and 10 of the 227 cultivars from all other countries. 'Red Delicious' was frequent in pedigrees of cultivars from Pacific-Rim countries (17 of 47)) and from the United States (26 of 115).

Of 439 cultivars and selections sampled, 41% of those released before 1930 was related to at least one of the five main founding clones. This increased to 74% during 1940–60 and remained at 73% in recent releases.

These results support Brown's concern (1973) about the trend in excessive use of 'Cox's Orange Pippin', 'Golden Delicious', 'Jonathan', 'Red Delicious', and 'McIntosh' as parents. The problem of restricted number of founding clones in apple breeding is common to many fruit crops, such as raspberry (Dale et al., 1993), blueberry (Hancock and Siefker, 1982), and peach (Scorza et al., 1988). The predominance of only five founding clones in modern apple cultivars may be explained by the lack of information on the breeding value of apple germplasm, which deters breeders from using untested parents. Cultivars such as 'Golden Delicious', 'Red Delicious', 'Jonathan', 'McIntosh', and 'Cox's Orange Pippin' have been reported to be generally valuable parents (Davis et al., 1954; Lantz, 1936). 'Red Delicious' seems to transmit red color, while 'Cox's Orange Pippin' and 'Golden Delicious' are useful to breed yellow and green apples (Brown, 1992; Percival and Proctor, 1994). In addition, mutants of 'Red Delicious', 'McIntosh', and 'Golden Delicious' are used in breeding for compact, spur-type, and dwarf growth habits (Brown, 1992).

Coancestry of apples. The mean coefficients of coancestry (Table 2) of the 77 cultivars included in this study were 0.101 with 'Golden Delicious', 0.058 with 'Red Delicious', 0.055 with 'Jonathan', 0.044 with 'McIntosh', and 0.022 with 'Cox's Orange Pippin'. Coefficients of coancestry ranged between 0 for most pairings to 0.281 for 'GoldRush' with 'Golden Delicious' and 'Novamac' with 'McIntosh'. The high levels of coancestry found

Table 3. Coefficients of coancestry of 50 world main-stream apple cultivars released since 1970.[z]

Clone	Akane	Akita Gold	Aori	Arlet	Burgundy	Chantecler	Charden	Cloden	Delcorf	Delrouval	Earlidel	Elan	Elstar	Empress	Falstaff	Feleac	Fiesta	Fushuai	Generos	Goldsmith	Greensleeves	Himekami	Hokuto	Honeycrisp	Hongbaoshi	Huaguan	Huashuai
Akane	500	-	-	63	63	-	-	-	-	250	-	-	-	63	-	125	63	-	63	-	-	125	-	-	-	-	-
Akita Gold	-	500	125	125	-	125	125	125	125	63	63	125	125	-	125	-	-	125	-	125	125	125	188	63	125	250	188
Aori	-	125	500	125	-	125	125	125	125	63	-	125	125	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Arlet	63	125	63	500	31	125	125	125	125	94	-	125	125	31	125	63	125	125	31	125	125	63	63	63	-	125	-
Burgundy	63	-	-	31	500	-	-	-	-	31	16	-	-	53	-	63	31	16	31	-	-	63	-	63	-	-	-
Chantecler	-	125	63	125	-	500	250	250	125	63	-	125	125	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Charden	-	125	63	125	-	250	500	250	125	63	-	125	125	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Cloden	-	125	63	125	-	250	250	500	125	63	-	125	125	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Delcorf	-	125	63	125	-	125	125	125	500	250	-	125	125	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Delrouval	250	63	31	94	31	63	63	63	250	500	-	63	63	31	63	63	31	63	31	63	63	63	31	31	-	63	-
Earlidel	-	63	125	-	16	-	-	-	-	-	500	-	-	55	-	-	-	125	-	-	-	63	63	31	125	63	188
Elan	-	125	63	125	-	125	125	125	125	63	-	500	125	-	250	-	-	125	-	125	250	-	63	63	-	125	-
Elstar	-	125	63	125	-	125	125	125	125	63	-	125	500	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Empress	63	-	-	31	53	-	-	-	-	31	55	-	-	523	-	63	31	47	31	-	-	63	-	47	-	-	-
Falstaff	-	125	63	125	-	125	125	125	125	63	-	250	125	-	500	-	-	125	-	125	250	-	63	63	-	125	-
Feleac	125	-	-	63	63	-	-	-	-	63	-	-	-	63	-	500	63	-	63	-	-	125	-	-	-	-	-
Fiesta	63	-	-	125	31	-	-	-	-	31	-	-	-	31	-	63	500	-	31	-	-	63	-	-	-	-	-
Fushuai	-	125	63	125	16	125	125	125	125	63	125	125	125	55	125	-	-	500	-	125	125	-	63	94	-	125	-
Generos	63	-	-	31	31	-	-	-	-	31	-	-	-	31	-	63	31	-	500	-	-	63	-	-	-	-	-
Goldsmith	-	125	63	125	-	125	125	125	125	63	-	125	125	-	125	-	-	125	-	500	125	-	63	63	-	125	-
Greensleeves	-	125	63	125	-	125	125	125	125	63	-	250	125	-	250	-	-	125	-	125	500	-	63	63	-	125	-
Himekami	125	125	63	63	63	-	-	-	-	63	63	-	-	63	-	125	63	-	63	-	-	500	125	-	125	125	188
Hokuto	-	188	125	63	-	63	63	63	63	31	63	63	63	-	63	-	-	63	-	63	63	125	500	31	125	188	188
Honeycrisp	-	63	31	63	63	63	63	63	63	31	31	63	63	43	63	-	-	94	-	63	63	-	31	500	-	63	-
Hongbaoshi	-	125	125	-	-	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	-	125	125	-	500	125	250
Huaguan	-	250	125	125	-	125	125	125	125	63	63	125	125	-	125	-	-	125	-	125	125	125	188	63	125	500	188
Huashuai	-	188	188	-	-	-	-	-	-	-	188	-	-	-	-	-	-	-	-	-	-	188	188	-	250	188	625
Jinghuang	-	125	125	-	-	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	-	125	125	-	250	125	250
Jubile	-	125	63	125	-	125	125	125	125	63	-	125	125	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Jupiter	-	63	125	-	-	-	-	-	-	-	125	-	-	-	-	-	125	-	-	-	-	63	63	-	125	63	188
Karmijn	125	-	-	63	63	-	-	-	-	63	-	-	-	63	-	125	188	-	63	-	-	125	-	-	-	-	-
Kent	125	-	-	63	63	-	-	-	-	63	-	-	-	63	-	125	188	-	63	-	-	125	-	-	-	-	-
Kogetsu	125	125	63	188	63	125	125	125	125	125	-	125	125	63	125	125	63	125	63	125	125	125	63	63	-	125	-
Korona	-	-	-	-	47	-	-	-	-	-	31	-	-	43	-	-	-	31	-	-	-	-	-	31	-	-	-
Luxiangziao	-	125	94	63	-	63	63	63	63	31	63	63	63	-	63	-	-	63	-	63	63	63	94	31	125	125	125
Michinoku	31	109	78	94	8	94	94	94	94	63	47	94	94	21	94	-	-	109	-	94	94	16	63	63	31	109	47
Pink Lady	-	125	63	125	-	125	125	125	125	63	-	125	125	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Predgornoe	-	63	125	-	-	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	-	63	63	-	125	63	188
Qinguan	-	188	125	125	-	125	125	125	125	63	63	125	125	-	125	-	-	125	-	125	125	63	125	63	125	188	125
Rubinovoe Duki	125	-	-	63	63	-	-	-	-	63	-	-	-	63	-	125	63	-	63	-	-	125	-	-	-	-	-
Sansa	250	78	63	94	31	63	63	63	63	156	31	63	63	31	63	63	63	63	31	63	63	78	47	31	31	78	47
Scarlet	250	63	125	31	31	-	-	-	-	125	125	-	-	31	-	63	31	-	31	-	-	125	63	-	125	63	188
Senshu	-	188	94	63	-	63	63	63	63	31	63	63	63	-	63	-	-	63	-	63	63	125	188	31	125	188	188
Shamrock	-	125	63	125	31	125	125	125	125	63	63	125	125	86	125	-	-	188	-	125	125	-	63	125	-	125	-
Skifskoe	-	125	63	188	-	125	125	125	125	63	-	125	125	-	125	-	63	125	-	125	125	-	63	63	-	125	-
Summerdel	-	63	125	-	-	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	-	63	63	-	125	63	188
Sundowner	-	125	63	125	-	125	125	125	125	63	-	125	125	-	125	-	-	125	-	125	125	-	63	63	-	125	-
Suntan	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	-
Vista Bella	-	-	-	-	12	-	-	-	-	-	47	-	-	291	-	-	-	47	-	-	-	-	-	23	-	-	-
Yanshanhong	-	125	125	-	-	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	-	125	125	-	250	125	250
Mean[x]	37	90	64	76	17	64	64	64	63	55	39	64	59	25	64	25	27	67	13	59	64	56	62	36	46	90	59
Mean[w]	47	100	74	86	27	74	74	74	73	65	49	74	69	36	74	35	37	77	23	69	74	66	72	46	56	100	72

[z]Coefficients of coancestry values × 1000; self-pollinated = 500; parent-offspring = 250; full sibs = 250; half sibs = 125; first cousins = 63. No coancestry of known parents indicated with dashes.

[x]Mean coefficient of coancestry excluding selfing.

[w]Mean coefficient of coancestry including selfing.

between many modern cultivars and 'Golden Delicious', 'Red Delicious', 'Jonathan', 'McIntosh', and 'Cox's Orange Pippin' indicate that further use of the five founding clones or their descendants will increase the risk of inbreeding in future generations.

Coefficients of coancestry among all 77 cultivars are shown in Tables 3, 4, and 5. The mean coancestry within cultivars in the mainstream (Table 3) and *Vf*-carrier (Table 4) groups was similar (0.051 and 0.050, respectively). Mean coancestry coefficients ranged from 0.006 to 0.090 in the first group and from 0.017 to 0.088 in the second group. The mean coancestry (Table 5) between the mainstream and the *Vf*-carrier group was more than half (0.032) of that found for each group and ranged from 0.009 to 0.092. Mean coancestry of the 77 selected apple cultivars was comparable with coancestry in plums (0.069 to 0.080) (Byrne, 1989) but was low compared with average coancestry reported in peaches (0.023 to 0.208, 0.034 to 0.330) (Scorza et al., 1985)..

Coancestry between mainstream cultivars (Table 3) was generally higher than coancestry between *Vf*-carrier cultivars (Table 4). About 25% of parental combinations in the first group had coefficients of coancestry ≥0.125 (selfings excluded) against 8% in the second group. About 5% of parental combinations between both groups (Table 5) showed coefficients of coancestry >0.125. These results indicate that pedigrees should be carefully examined before

Table 3. Continued.

Clone	Jinghuang	Jubile	Jupiter	Karmijn	Kent	Kogetsu	Korona	Luxiangziao	Michinoku	Pink Lady	Predgornoe	Qinguan	Rubinovoe Duki	Sansa	Scarlet	Senshu	Shamrock	Skifskoe	Summerdel	Sundowner	Suntan	Vista Bella	Yanshanhong	Mean [x]	Mean [w]
Akane	-	-	-	125	125	125	-	-	31	-	-	-	125	250	250	-	-	-	-	-	-	-	-	37	47
Akila Gold	125	125	63	-	-	125	-	125	109	125	63	188	-	78	63	188	125	125	63	125	-	-	125	90	100
Aori	-	63	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	58	68
Ariel	-	125	-	63	63	188	-	63	94	125	-	125	63	94	31	63	125	188	-	125	-	-	-	74	84
Burgundy	-	-	-	63	63	63	47	-	8	-	-	-	63	31	31	-	31	-	-	-	-	12	-	17	27
Chantecler	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	63	73
Charden	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	63	73
Cloden	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	63	73
Delcorf	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	62	72
Delrouval	-	63	-	63	63	125	-	31	63	63	-	63	63	156	125	31	63	63	-	63	-	-	-	54	64
Earlidel	125	-	125	-	-	-	31	63	47	-	125	63	-	31	125	63	63	-	125	-	-	47	125	41	51
Elan	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	63	73
Elstar	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	58	68
Empress	-	-	-	63	63	63	47	-	23	-	-	-	63	31	31	-	94	-	-	-	-	291	-	25	36
Falstaff	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	63	73
Feleac	-	-	-	125	125	125	-	-	-	-	-	-	125	63	63	-	-	-	-	-	-	-	-	25	35
Fiesta	-	-	125	188	188	63	-	-	-	-	-	-	63	63	31	-	-	63	-	-	125	-	-	27	37
Fushuai	-	125	-	-	-	125	31	63	109	125	-	125	-	63	-	63	188	125	-	125	-	47	-	66	76
Generos	-	-	-	63	63	63	-	-	-	-	-	-	63	31	31	-	-	-	-	-	-	-	-	13	23
Goldsmith	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	58	68
Greensleeves	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	63	73
Himekami	125	-	63	125	125	125	-	63	16	-	63	63	125	78	125	125	-	-	63	-	-	-	125	57	67
Hokuto	125	63	63	-	-	63	-	94	63	63	63	125	-	47	63	188	63	63	63	63	-	-	125	63	73
Honeycrisp	-	63	-	-	-	63	31	31	63	63	-	63	-	31	-	31	125	63	-	63	-	23	-	36	46
Hongbaoshi	250	-	125	-	-	-	-	125	31	-	125	125	-	31	125	125	-	-	125	-	-	-	250	49	59
Huaguan	125	125	63	-	-	125	-	125	109	125	63	188	-	78	63	188	125	125	63	125	-	-	125	90	100
Huashuai	250	-	188	-	-	-	-	125	47	-	188	125	-	47	188	188	-	-	188	-	-	-	250	63	76
Jinghuang	500	-	125	-	-	-	-	125	31	-	125	250	-	31	125	125	-	-	125	-	-	-	250	51	61
Jubile	-	500	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	125	-	125	-	-	-	58	68
Jupiter	125	-	500	125	125	-	-	63	31	-	125	63	-	63	125	63	-	-	125	-	125	-	125	44	54
Karmijn	-	-	125	500	250	125	-	-	-	-	-	-	125	94	63	-	-	-	-	-	125	-	-	36	46
Kent	-	-	125	250	500	125	-	-	-	-	-	-	125	94	63	-	-	-	-	-	125	-	-	36	46
Kogetsu	-	125	-	125	125	500	-	63	94	125	-	125	125	125	63	63	125	125	-	125	-	-	-	83	93
Korona	-	-	-	-	-	-	500	-	16	-	-	-	-	-	-	-	63	-	-	-	-	23	-	6	16
Luxiangziao	125	63	63	-	-	63	-	500	63	63	63	125	-	47	63	94	63	63	63	63	-	-	125	55	65
Michinoku	31	94	31	-	-	94	16	63	531	94	31	109	-	70	47	63	125	94	31	94	-	12	31	57	68
Pink Lady	-	125	-	-	-	125	-	63	94	500	-	125	-	63	-	63	125	125	-	250	-	-	-	61	71
Predgornoe	125	-	125	-	-	-	-	63	31	-	500	63	-	31	125	63	-	-	125	-	-	-	125	34	44
Qinguan	250	125	63	-	-	125	-	125	109	125	63	500	-	78	63	125	125	125	63	125	-	-	125	86	96
Rubinovoe Duki	-	-	-	125	125	125	-	-	-	-	-	-	500	63	63	-	-	-	-	-	-	-	-	25	35
Sansa	31	63	63	94	94	125	-	47	70	63	31	78	63	500	156	47	63	63	31	63	31	-	31	63	73
Scarlet	125	-	125	63	63	63	-	63	47	-	125	63	63	156	500	63	-	-	125	-	-	-	125	55	65
Senshu	125	63	63	-	-	63	-	94	63	63	63	125	-	47	63	500	63	63	63	63	-	-	125	62	72
Shamrock	-	125	-	-	-	125	63	63	125	125	-	125	-	63	-	63	500	125	-	125	-	47	-	67	77
Skifskoe	-	125	-	-	-	125	-	63	94	125	-	125	-	63	-	63	125	500	-	125	-	-	-	61	71
Summerdel	125	-	125	-	-	-	-	63	31	-	125	63	-	31	125	63	-	-	500	-	-	-	125	34	44
Sundowner	-	125	-	-	-	125	-	63	94	250	-	125	-	63	-	63	125	125	-	500	-	-	-	61	71
Suntan	-	-	125	125	125	-	-	-	-	-	-	-	-	31	-	-	-	-	-	-	500	-	-	11	21
Vista Bella	-	-	-	-	-	-	23	-	12	-	-	-	-	-	-	-	47	-	-	-	-	535	-	10	21
Yanshanhong	250	-	125	-	-	-	-	125	31	-	125	125	-	31	125	125	-	-	125	-	-	-	500	49	59
Mean x	49	58	42	36	36	84	6	55	58	62	31	86	25	63	52	62	68	62	31	62	11	10	46	51	
Mean [w]	59	68	52	46	46	94	16	65	68	72	41	96	35	73	62	72	78	72	41	72	21	21	56		61

selecting parents. With increasing demands for disease-resistant cultivars, future apple cultivars will not solely derive from intermating individuals within the mainstream group. However, with the high coefficients of coancestry between many individuals from the mainstream and *Vf*-carrier groups (Table 5), the latter group provides only a short-term solution. In addition, report of a new race of apple scab virulent to all *Vf* gene cultivars and selections tested (Parisi et al., 1993) reinforces the need for other sources of scab resistance. It is essential in future to introduce new germplasm into breeding programs and combine resistances to several diseases and pests.

Inbreeding coefficients. Among cultivars sampled, 6% showed an inbreeding coefficient >0. Inbreeding coefficients ranged from 0 for most cultivars to 0.297 for 'Dayton'. The inbreeding coefficients of 'Tydeman's Late Orange', 'Sinta', 'Enterprise', 'Howgate Wonder', 'Mellow', and 'Webster' were all 0.250. For the 77 modern cultivars studied, four of the 50 mainstream cultivars and nine of the 27 *Vf*-carrier cultivars were inbred (Table 2). Mean inbreeding coefficients were 0.01 for cultivars in the mainstream group and 0.04 for cultivars in the *Vf*-carrier group. Overall, the inbreeding level in apple is low compared with other fruit crops such as peach (0.26 to 0.35) (Scorza et al., 1988), blueberry (0.13) (Hancock and Siefker, 1982), and raspberry (0.12) (Dale et al., 1993). Mean inbreeding coefficients in apple are similar to those reported in plums (0.02 to 0.05) (Byrne, 1989). However mean coefficients of coancestry of the 77 apple cultivars sampled were 2 to 5 times their mean inbreeding coefficients. Consequently, even if inbreeding in apple is not a problem in this generation, the coancestry level of many future potential parents indicates that problems may arise in the next generation.

Little is known about the effects of inbreeding in apple. It has increased the juvenile period of progenies related to 'Cox's Orange

Table 4. Coefficients of coancestry of 27 world vf-carrier apple cultivars released since 1970.[z]

Clone	Baujade	Britegold	Dayton	Delorina	Enterprise	Florina	Freedom	Goldrush	Jolana [y]	Jonafree	Liberty [y]	McShay	Moira	Novamac	Pionier	Priam	Prima	Priscilla	Redfree	Retina [y]	Rewena [y]	Selena	Sir Prize	Trent	Vanda [y]	Voinea	William's Pride	Mean [x]	Mean [w]
Baujade	500	5	8	8	17	17	33	55	-	25	-	17	10	6	18	33	35	17	6	10	10	18	80	10	-	18	12	17	36
Britegold	5	500	70	36	72	72	27	17	16	42	16	72	66	66	43	51	55	88	35	20	20	59	20	66	8	27	47	41	60
Dayton	8	70	648	23	63	47	43	12	23	43	23	63	94	145	139	63	246	39	98	31	31	170	31	94	12	123	116	68	92
Delorina	8	36	23	500	63	250	18	35	-	60	-	31	41	21	41	94	20	40	21	10	10	10	33	41	-	10	27	35	53
Enterprise	17	72	63	63	625	125	66	55	63	41	63	188	145	152	35	63	70	143	27	20	20	66	66	145	31	35	47	70	93
Florina	17	72	47	250	125	500	35	70	-	119	-	63	82	43	82	188	39	80	43	20	20	20	66	82	-	20	55	61	79
Freedom	33	27	43	18	66	35	500	80	16	53	63	66	70	59	43	70	86	51	27	43	43	51	133	70	8	43	39	49	68
Goldrush	55	17	12	35	55	70	80	531	-	188	-	55	18	10	49	109	82	56	10	10	10	41	221	18	-	41	28	47	67
Jolana [y]	-	16	23	-	63	-	16	-	500	-	31	63	63	70	8	-	16	31	8	-	-	23	-	63	250	8	16	28	47
Jonafree	25	42	43	60	41	119	53	188	-	533	-	41	68	37	68	145	59	42	37	29	29	29	100	68	-	29	48	52	72
Liberty [y]	-	16	23	-	63	-	63	-	31	-	500	63	63	70	8	-	16	31	8	-	-	23	-	63	16	8	16	21	40
McShay	17	72	63	31	188	63	66	55	63	41	63	500	145	152	35	63	70	143	27	20	20	66	66	145	31	35	47	66	85
Moira	10	66	94	41	145	82	70	18	63	68	63	145	500	180	70	102	78	82	55	39	39	70	39	195	31	39	74	72	91
Novamac	6	66	145	21	152	43	59	10	70	37	70	152	180	531	64	55	98	82	86	23	23	96	23	180	35	49	109	72	91
Pionier	18	43	139	41	35	82	43	49	8	68	8	35	70	64	500	102	258	27	49	23	23	145	70	70	4	129	62	62	80
Priam	33	51	63	94	63	188	70	109	-	145	-	63	102	55	102	500	78	35	55	39	39	39	133	102	-	39	70	65	84
Prima	35	55	246	20	70	39	86	82	16	59	16	70	78	98	258	78	516	55	66	47	47	289	141	78	8	258	85	88	107
Priscilla	17	88	39	40	143	80	51	56	31	42	31	143	82	82	27	35	55	500	20	20	20	43	66	82	16	27	31	51	69
Redfree	6	35	98	21	27	43	27	10	8	37	8	27	55	86	49	55	66	20	500	23	23	49	23	55	4	33	78	36	54
Retina [y]	10	20	31	10	20	20	43	10	-	29	-	20	39	23	23	39	47	20	23	500	70	23	39	39	-	23	23	24	42
Rewena [y]	10	20	31	10	20	20	43	10	-	29	-	20	39	23	23	39	47	20	23	70	500	23	39	39	-	23	23	24	42
Selena	18	59	170	10	66	20	51	41	23	29	23	66	70	96	145	39	289	43	49	23	23	531	70	70	12	145	68	64	83
Sir Prize	80	20	31	33	66	66	133	221	-	100	-	66	39	23	70	133	141	66	23	39	39	70	625	39	-	70	47	60	83
Trent	10	66	94	41	145	82	70	18	63	68	63	145	195	180	70	102	78	82	55	39	39	70	39	500	31	39	74	72	91
Vanda [y]	-	8	12	-	31	-	8	-	250	-	16	31	31	35	4	-	8	16	4	-	-	12	-	31	500	4	8	19	37
Voinea	18	27	123	10	35	20	43	41	8	29	8	35	39	49	129	39	258	27	33	23	23	145	70	39	4	500	42	49	67
William's Pride	12	47	116	27	47	55	39	28	16	48	16	47	74	109	62	70	85	31	78	23	23	68	47	74	8	42	515	48	67
Mean [x]	17	41	68	35	70	61	49	47	28	52	21	66	72	72	62	65	88	51	36	24	24	64	60	72	19	49	48	50	
Mean [w]	36	60	92	53	93	79	68	67	47	72	40	85	91	91	80	84	107	69	54	42	42	83	83	91	37	67	67		70

[z]Coefficients of coancestry values × 1000. Self-pollinated = 500; parent-offspring = 250; full sibs = 250; half sibs = 125; first cousins = 63. No coancestry of known parents indicated with dashes.

[y]Cultivars with incomplete parentage.

[x]Mean coefficient of coancestry excluding selfing.

[w]Mean coefficient of coancestry including selfing.

Pippin' and has reduced their vigor and survival rate (Brown, 1973). It can be a useful strategy for the production of commercial cultivars, especially if the relationship between inbreeding coefficients and traits of interest is known. However inbreeding also increases uniformity within progenies which may jeopardize future improvement (Lesley, 1957). The role of inbreeding in apple breeding needs to be studied both for short-term commercial cultivar production and for long-term population improvement.

Status effective number. The status effective numbers were 8.2 for the 50 mainstream cultivars (Table 3) , 7.1 for the 27 *Vf*-carrier cultivars (Table 4), and 10.2 for the 77 cultivars of both groups analyzed together (Table 5). This means that genetic diversity in each of these three groups is reduced to the equivalent of 8, 7, and 10 panmictic-mated, unrelated, and noninbred genotypes, respectively. Such small status effective numbers indicate that breeders are working with a very narrow genetic base.

The status effective number is a useful quantitative measure of the current state of genetic diversity in a breeding population and extends information given by inbreeding and coancestry coefficients (Lindgren et al., 1995). It can be calculated easily for any population from a coancestry matrix and will assist breeders in assessing the germplasm they are using. For example, status effective numbers, calculated from published results, were 2.6 to 4.4 in peach (Scorza et al., 1985) and 6.3 to 7.2 in plums (Byrne, 1989).

Despite the availability of large numbers of modern cultivars and breeding selections from apple breeding programs, worldwide, the actual size of the genetic resources currently used by breeders is small and, in the course of future genetic improvement, may become exhausted. This loss of genetic diversity will result in a preponderance of genes from the main founding clones, while genes from other germplasm will disappear. There is a great need to broaden the genetic base for breeding new apple cultivars. Modified backcross mating design has been used by many breeders to minimize loss of genetic diversity, particularly for the development of scab-resistant apple cultivars carrying the *Vf* gene (Williams et al., 1967, 1975, 1984). However, the genetic base from which these recurrent parents are chosen is still narrow.

One strategy followed in New Zealand since 1989 (Noiton and Shelbourne, 1992) is to use recurrent selection for combining ability to develop an apple breeding population. Such strategy is used by most forest tree breeding programs. The apple breeding population was established from open-pollinated seeds of 500 cultivars collected from clonal repositories throughout the world. This strategy will increase and maintain a high level of diversity for the sustainable improvement of a large number of useful traits.

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Table 5. Coefficients of coancestry of 77 world apple cultivars released since 1970.[z]

Clone	Baujade	Britegold	Dayton	Delorina	Enterprise	Florina	Freedom	Goldrush	Jolana[y]	Jonafree	Liberty[y]	McShay	Moira	Novamac	Pionier	Priam	Prima	Priscilla	Redfree	Retina[y]	Rewena[y]	Selena	Sir Prize	Trent	Vanda[y]	Voinea	William's Pride	Mean
Akane	-	31	31	63	-	125	-	16	-	78	-	-	63	31	63	125	-	-	31	-	-	-	-	63	-	-	39	28
Akita Gold	47	31	-	31	63	63	63	148	-	55	-	63	-	-	31	63	63	94	-	-	-	31	188	-	-	31	16	40
Aori	23	63	-	39	78	78	31	86	-	39	-	78	-	-	16	31	31	141	-	-	-	16	94	-	-	16	8	32
Arlett	47	16	16	47	31	94	63	148	-	86	-	31	31	16	63	125	63	31	16	-	-	31	188	31	-	31	35	46
Burgundy	4	31	59	35	39	70	78	12	16	51	63	39	78	66	51	78	39	23	35	20	20	27	16	78	8	20	43	41
Chantecler	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Charden	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Cloden	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Delcorf	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Delrouval	23	16	16	39	16	78	31	78	-	63	-	16	31	16	47	94	31	16	16	-	-	16	94	31	-	16	27	30
Earlidel	-	78	23	31	125	63	16	16	31	16	31	125	63	70	8	-	16	156	8	-	-	23	-	63	16	8	27	37
Elan	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Elstar	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Empress	-	49	68	31	86	63	21	8	43	39	43	86	117	119	49	63	35	43	33	-	-	51	-	117	21	18	82	48
Falstaff	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Feleac	-	31	31	63	-	125	-	16	-	78	-	-	63	31	63	125	-	-	31	-	-	-	-	63	-	-	39	28
Fiesta	-	16	16	31	-	63	-	8	-	39	-	-	31	16	31	63	-	-	16	63	63	-	-	31	-	-	20	19
Fushuai	47	16	23	16	94	31	78	141	31	47	31	94	63	70	39	63	78	63	8	-	-	55	188	63	16	39	43	53
Generos	-	16	16	31	-	63	-	8	-	39	-	-	31	16	31	63	-	-	16	-	-	-	-	31	-	125	20	19
Goldsmith	172	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	36
Greensleeves	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Himekami	-	63	31	78	31	156	-	23	-	86	-	31	63	31	63	125	-	63	31	-	-	-	-	63	-	-	39	36
Hokuto	23	31	-	23	47	47	31	78	-	31	-	47	-	-	16	31	31	78	-	-	-	16	94	-	-	16	8	24
Honeycrisp	23	16	23	8	78	16	94	70	31	23	125	78	63	70	23	31	47	47	8	-	-	39	94	63	16	23	23	42
Hongbaoshi	-	63	-	31	63	63	-	16	-	16	-	63	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	16
Huaguan	47	31	-	31	63	63	63	148	-	55	-	63	-	-	31	63	63	94	-	-	-	31	188	-	-	31	16	40
Huashuai	-	94	-	47	94	94	-	23	-	23	-	94	-	-	-	-	-	188	-	-	-	-	-	-	-	-	-	24
Jinghuan	-	63	-	31	63	63	-	16	-	16	-	63	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	16
Jubilee	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Jupiter	-	63	-	31	63	63	-	16	-	16	-	63	-	-	-	-	-	125	-	63	63	-	-	-	-	-	-	21
Karmijn	-	31	31	63	-	125	-	16	-	78	-	-	63	31	63	125	-	-	31	63	63	-	-	63	-	-	39	33
Kent	-	31	31	63	-	125	-	16	-	78	-	-	63	31	63	125	-	-	31	63	63	-	-	63	-	-	39	33
Kogetsu	47	31	31	78	31	156	63	156	-	125	-	31	63	31	94	188	63	31	31	-	-	31	188	63	-	31	55	60
Korona	4	23	55	4	70	8	31	4	31	12	31	70	78	86	23	16	47	39	23	16	16	39	16	78	16	23	31	33
Luxiangziao	23	31	-	23	47	47	31	78	-	31	-	47	-	-	16	31	31	78	-	-	-	16	94	-	-	16	8	24
Michinoku	35	23	12	20	70	39	55	109	16	39	16	70	31	35	27	47	55	70	4	-	-	35	141	31	8	27	20	38
Pink Lady	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Predgornoe	-	63	-	31	63	63	-	16	-	16	-	63	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	16
Qinguan	47	31	-	31	63	63	63	148	-	55	-	63	-	-	31	63	63	94	-	-	-	31	188	-	-	31	16	40
Rubinovoe Duki.	-	31	31	63	-	125	-	16	-	78	-	-	63	31	63	125	-	-	31	-	-	-	-	63	-	-	39	28
Sansa	23	31	16	47	31	94	31	82	-	66	-	31	31	16	47	94	31	47	16	16	16	16	94	31	-	16	27	35
Scarlet	-	78	16	63	63	125	-	23	-	55	-	63	31	16	31	63	-	125	16	-	-	-	-	31	-	-	20	30
Senshu	23	31	-	23	47	47	31	78	-	31	-	47	-	-	16	31	31	78	-	-	-	16	94	-	-	16	8	24
Shamrock	47	31	47	16	156	31	94	141	63	47	63	156	125	141	47	63	94	94	16	-	-	78	188	125	31	47	47	73
Skifskoe	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Summerdel	-	63	-	31	63	63	-	16	-	16	-	63	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	16
Sundowner	47	-	-	16	31	31	63	141	-	47	-	31	-	-	31	63	63	31	-	-	-	31	188	-	-	31	16	32
Suntan	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	63	63	-	-	-	-	-	-	5
Vista Bella	-	35	59	-	47	-	12	-	23	-	23	47	47	66	20	-	39	23	20	-	-	55	-	47	12	20	93	25
Yanshanhong	-	63	-	31	63	63	-	16	-	16	-	63	-	-	-	-	-	125	-	-	-	-	-	-	-	-	-	16
Mean	25	29	14	31	45	61	36	76	6	45	9	45	26	21	31	58	35	57	9	7	7	21	92	26	3	20	23	32

[z]Coefficients of coancestry values × 1000; self-pollinated = 500; parent-offspring = 250; full sibs = 250; half sibs = 125; first cousins = 63. No coancestry of known parents indicated with dashes.

[y]Cultivars with incomplete parentage.

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