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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.

| Cultivar | Inbreeding coefficients | Coefficient of coancestry with 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

| 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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