

Heritability and Patterns of Inheritance of the Ripening Date of Apples

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Abstract. A major objective of the apple (*Malus domestica* Borkh.) breeding program in Stanthorpe, Australia, is to develop early ripening, high-quality cultivars. The heritability and inheritance of ripening date was investigated. Regression of offspring on midparent harvest dates and estimation of best linear unbiased predictions for parents were used to demonstrate that apple harvest date is highly heritable. Predominantly, additive genetic components of variance are responsible for the variation. Despite the existence of some specific combining ability variance and some non-normal family distributions, the best strategy for a breeder to predict the harvest date of progeny is to calculate the mean harvest date of parents.

Apple breeding is a long-term and costly process due to the long juvenility period and the large size of mature apple trees. However, because apples are vegetatively propagated, a selected cultivar is genetically fixed and can have industry use for hundreds of years (Brown, 1975).

Stanthorpe is Australia's earliest apple production district, and a breeding program was initiated to enhance this market advantage. The Queensland Dept. of Primary Industries began apple breeding at Stanthorpe in 1964 to produce new red dessert cultivars that matured before 'Jonathan', the standard early cultivar, and that were of a higher quality than the commercially available early cultivars. Because the eating quality of early season apples is often inferior to that of mid- and late-season apples, the breeding plan had the two parallel objectives of earliness and high eating quality. Three cultivars that mature before 'Jonathan' have been released from the Stanthorpe program: 'Earlidel', 'Summerdel', and 'GB 63-43' (Tancred et al., 1994).

Because quantitative studies of fruit genetics have usually been done retrospectively from breeding program data, they often lack a specific design for estimation of heritability.

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This, too, is the case for the Stanthorpe program. However, genetic parameters have been usefully estimated in this manner for several tree fruit crops (Abe et al., 1993; Dicenta et al., 1993; Hansche et al., 1966, 1972a, 1972b; Thompson and Baker, 1993), and we adopt a similar strategy.

Only a few studies have been made of apple ripening date, and they all concluded it showed polygenetic inheritance. Crane and Lawrence (1933) observed that no sharply discontinuous variation occurred and that the majority of progeny ripened between the parents. Howlett and Gourley (1946), Bishop (1951), and Davis et al. (1954) concurred with this finding, but Hartman and Howlett (1942) found transgressive segregation with a considerable percentage of progenies earlier than the early parent and some later than the late parent. Brown (1960) found the progeny mean on average 2 weeks earlier than the midparent value, except for crosses involving very late parents, where the progeny mean was up to 2 months earlier than the midparent mean. Brown (1975) reviewed the breeding and genetics of apples and Brown (1992) has reviewed the inheritance of Mendelian traits in apples. Way et al. (1990) have described *Malus* spp. genetic diversity.

Breeders at Stanthorpe hoped that by hybridizing early ripening parents with high-fruit-quality parents, families would be generated that had a sufficient number of seedlings that matured before 'Jonathan', to enable selection to be made within these on fruit quality characters. This study reports the variation in ripening date within and among families pro-

duced in the Stanthorpe apple breeding program. Several quantitative methods that can be used as predictive selection tools are used. Fruit quality data will not be discussed here.

Materials and Methods

Parent cultivars and hybridizations. Biparental hybridizations were done among 13 early, mid-, or late-maturing apple cultivars from 1964 to 1970. The parents were selected from the best available in Australia at the time (Table 1). Two of the cultivars are full-sibs ('Milton' and 'Early McIntosh'), but no genetic relationship is known to exist between any of the others. Thirty-six families were produced with an average size of 286 individual trees (range 16 to 1100). The seedlings were field-planted between 1966 and 1971. Only two sets of reciprocal crosses were made, 'Milton' x 'Early McIntosh' and 'Golden Delicious' x 'Jonathan'.

Planting design. Because the primary aim was to select suitable cultivars for commercial use, there was no planned trial layout or replication for the purposes of this study. Trees within a family were planted beside each other in orchard rows each year. However, because several crosses were made over a number of years, complete families were not always planted together.

Population management. Seedlings were evaluated for ripening date every 2 to 5 days during the harvest period. Ripening date was determined by subjective assessment of fruit texture, flavor, blush color, and background color. Seedlings were culled or further propagated after several years of consistent performance. Seedling trees were observed cropping for 3 years, on average. About 16% of the seedlings planted never cropped and were disregarded in all calculations. Observations were made from 1973 to 1985, when the orchard was removed.

Seasonal adjustments. Due to weather variation between years, the harvest date for any particular genotype may vary from year to year. These year effects were considered to be fixed effects in the analyses. To account for these effects, each year was assigned an earliness or lateness factor from the harvest dates of standard cultivars on the research station and on district farms. This factor ranged from

Table 1. Ripening date of 13 apple cultivars used as parents at Stanthorpe, Australia. Ripening date expressed as day relative to 'Jonathan'.

Parental cultivar	Ripening date
Stark's Earliest	-45
Milton	-43
Early McIntosh	-37
Canterbury	-36
Ruby Gem	-34
Carrington Red	-33
William's Favourite	-30
Earlblaze	-26
Jonathan	0
Sayers	7
Delicious	10
Golden Delicious	22
Granny Smith	47

14 days early to 14 days late. For the 13 years of observation, it averaged 1.3 days early. Harvest dates of individual progeny within families were adjusted by this factor for each year. Harvest dates for each tree were then averaged across years. All harvest dates are expressed relative to that of 'Jonathan'.

Genetic analysis. The parents used spanned a wide range of maturity periods (Table 1) and were considered to constitute a random sample from the base population accessed by the Stanthorpe breeding program. Narrow-sense heritability (h^2) was estimated using the linear regression of year-adjusted offspring performance on the average performance of their parents, or midparent value (Falconer, 1989). Three procedures for estimating offspring midparent regression were investigated following Kempthorne and Tandon (1953) and Bohern et al. (1961): 1) the regression of the phenotypic mean of all offspring from a given biparental combination on the midparent value; 2) the regression of offspring on midparent, in which the midparent values were repeated for each of the progeny; and 3) the weighted regression technique of Kempthorne and Tandon (1953). As have been found by others, the results of each procedure were similar, and only the first procedure, the regression of the phenotypic mean of all offspring on the midparent value, is presented.

The assumption that the effects of environment are randomly distributed among the individuals, so that the environmental correlation between individuals in a progeny group is zero (Bohern et al., 1961), is unlikely to be fulfilled. However, since all progeny from a cross were not grown adjacent to each other, there is some protection against such environmental correlations. Nevertheless, any environmental correlations that do exist may increase the covariance among family members. Therefore, estimates of genetic parameters should be treated with some degree of care.

General combining ability (GCA) effects of the parents and specific combining ability (SCA) effects for all biparental combinations were obtained by applying the method of best linear unbiased prediction (BLUP). The mating design model is an incomplete diallel without reciprocals where:

$Y_{ijk} = \mu + g_j + g_k + s_{jk} + e_{ijk}$ and Y_{ijk} is the phenotypic observation for the i th progeny member of the family jk ; μ is the population mean; g_j is the random variable associated with the GCA of the j th female; g_k is the random variable associated with the GCA of the k th male; s_{jk} is the random variable associated with the SCA of the parents j and k ; e_{ijk} is the random error associated with the i th progeny member of the family jk .

Analyses were performed using Giesbrecht's algorithm of restricted maximum likelihood (Huber, 1993). The BLUP theory was developed specifically to analyze diverse and unbalanced performance data from dairy cattle (Henderson, 1963, 1973, 1977a, 1977b). The BLUP theory has successfully been adapted to predict future performance of par-

ents in forest tree breeding (White and Hodge, 1988). Forest tree breeding shares many of the experimental design problems found in apple breeding. The Wilk-Shapiro test was undertaken to test the normality of the data for each family (Proc. Univariate; SAS, 1990).

Results and Discussion

All the individual families showed continuous distribution around the midparent with

no evidence of segregation due to major gene effects. Thirteen of the 36 families had non-normal distributions, either due to excessive skewness or kurtosis. Examples of two normal and non-normally distributed families are shown in Fig. 1.

The mean harvest date of all progeny was -10.2 days, which was only 0.6 days earlier than the mean (weighted) of all midparents. On a family basis, the mean of the 36 families was -13.4 days, which was only 0.9 days

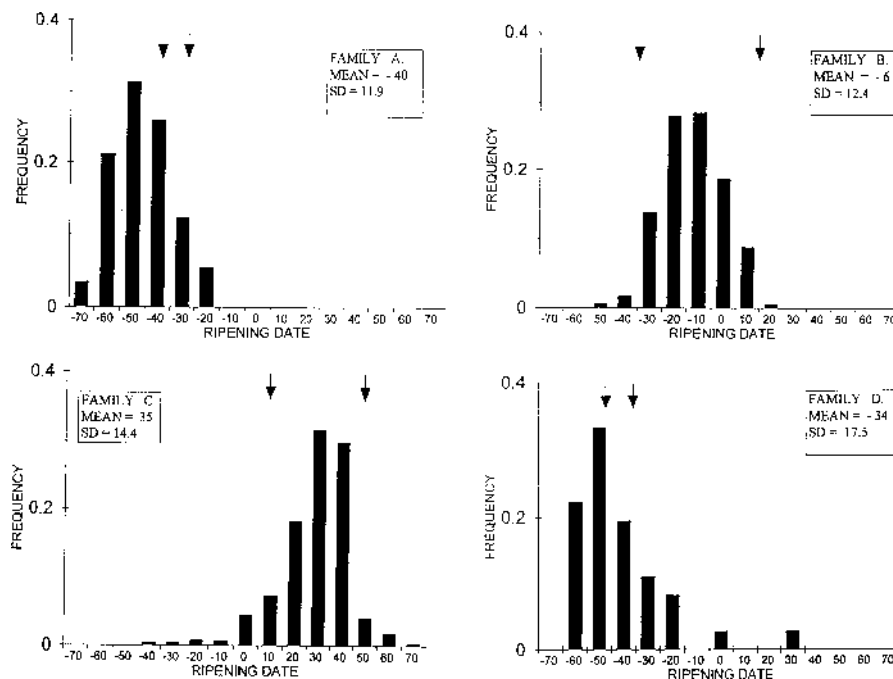


Fig. 1. Frequency distributions of ripening date in four families of apple seedlings: (A) 'William's Favourite' x 'Early McIntosh', (B) 'William's Favourite' x 'Golden Delicious', (C) 'Delicious' x 'Granny Smith', and (D) 'Milton' x 'Carrington Red'. Only families (A) and (B) have normal distributions. Arrows indicate parent cultivar ripening dates. Ripening date expressed as days relative to 'Jonathan'.

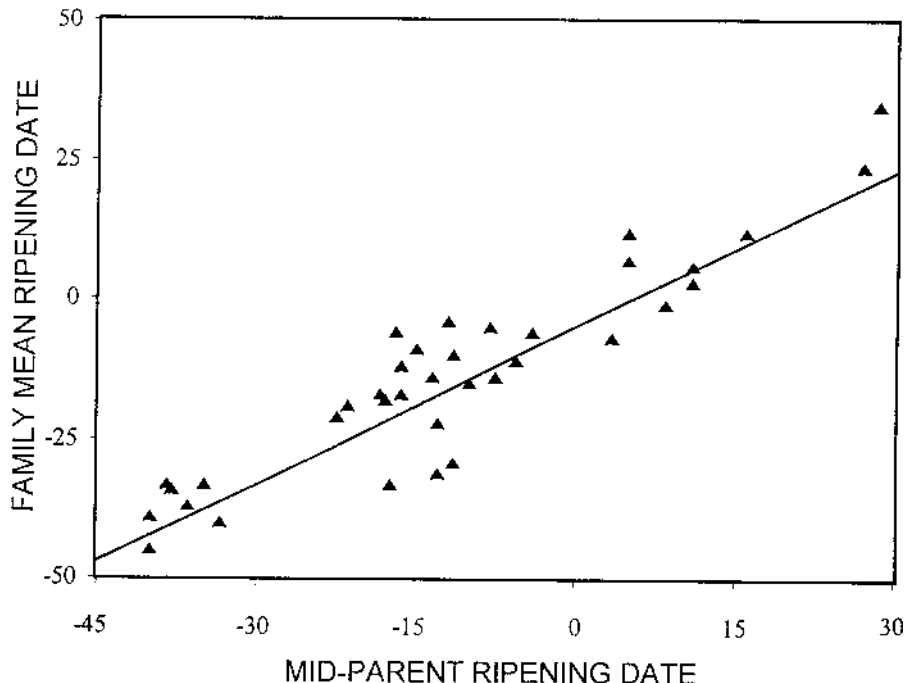


Fig. 2. Offspring midparent regressions of ripening date for 36 apple families. Ripening date expressed as days relative to 'Jonathan'. Regression equation: $y = 0.94x - 2.4$.

earlier than the average midparent harvest date. These average harvest dates are only slightly earlier than the midparent dates, which contrasts with the 2 weeks earlier reported by Brown (1960). The sample variation of all progeny was 438.7, and of all midparents, accounting for family size, it was 175.3.

Brown (1960) found that families from two late-ripening parents produced only a small proportion of their progeny as late ripening, a phenomenon we did not observe, possibly because only a few of these types of crosses were made in the Stanthorpe program. Brown (1975) proposed a minimum ripening date that was fixed by a minimum fruit development period after bloom. He used this relationship to explain why crosses between two early ripening parents would produce a population skewed toward lateness and with reduced variation. This result was absent with our early x early families, possibly because this theoretical limit of earliness was not yet reached.

Narrow-sense heritability (h^2) for harvest date was 0.94 ± 0.067 (Fig. 2), a relatively high value for a quantitative character, but consistent with the high estimates found for harvest date of Japanese pear (*Pyrus pyrifolia* Nakai) (Abe et al., 1993), sweet cherry (*Prunus avium* L.) (Hansche et al., 1966; Hansche and Brooks, 1965), peach (*Prunus persica* L. Batsch) (Hansche et al., 1972b), and walnut (*Juglans regia* L.) (Hansche et al., 1972a). Regression of Brown's (1960) apple cultivar progeny means on midparent values reveals that, in his data set, h^2 was 0.69 ± 0.071 .

Heritability, as we have measured it, can be overestimated if basic assumptions are violated. These commonly include the existence of dominance or epistatic genetic components or prior inbreeding within the parents (Falconer, 1989; Fernandez and Miller, 1985). The former is assumed to be low and the latter is known to be negligible amongst our parents. If significant genotype \times environment ($G \times E$) interaction exists, then maturity re-ranking will occur in different environments and years. Ignoring this $G \times E$ interaction will also cause h^2 to be overestimated. This hazard can be avoided by growing parents and offspring in different environments (Casler, 1982; Fernandez and Miller, 1985). This was the case in our experiments, where the parents were grown in a repository under better horticultural conditions than the progeny. Also, the year effects on progeny were reduced by adjusting for season, then averaging across years. Alternatively, if the variation differs between parents and offspring, then the regression can be done on standardized data (Frey and Horner, 1957). This procedure gave an estimate of heritability of 0.924 ± 0.065 , which is not different from that based on the year-adjusted data.

The high narrow-sense heritability we found for harvest date implies that additive gene effects are predominantly controlling inheritance. This finding is supported by the BLUP analysis where the variance component of GCA (237.8) was nearly 10 times the variance component of SCA (25.4). The GCA estimates (Table 2) can be used to predict the

Table 2. General combining ability (GCA) for ripening date of 13 apple cultivars used as parents.

Parental cultivar	GCA ²
Stark's Earliest	-16.13
Milton	-11.67
Early McIntosh	-9.27
Canterbury	-12.96
Ruby Gem	-0.21
Carrington Red	-6.69
William's Favourite	-9.62
Stark Earliblaze	-11.00
Jonathan	8.29
Sayers	3.98
Delicious	13.83
Golden Delicious	14.66
Granny Smith	36.78

²GCA expressed as ripening date relative to 'Jonathan'.

progeny mean of future crosses within the parental set. The rank order of parent ripening date and parent GCA is similar when these two variables are regressed, $r^2 = 0.91$.

The SCA effects of each cross (Table 3) indicate deviations from the expected progeny means as predicted by GCA. They have no use outside of the actual crosses from which they were measured, but their small size in relation to GCA effects supports the strong influence of additive genetic effects on the inheritance of maturity.

A knowledge of heritability and combining ability estimates can be useful when planning crosses for a specific ripening period; it can also be used to predict average ripening dates of crosses made for other objectives. Despite variable distributions within families, the best strategy for producing a population of early maturing apple seedlings is to cross cultivars that have an early midparent ripening date. A knowledge of the inheritance of fruit quality characteristics can then be applied to predict the range of fruit quality that will exist within families.

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Table 3. Specific combining abilities (SCA) of 36 apple crosses for ripening date. Ripening date expressed as days relative to 'Jonathan'.

Cross	SCA ²
Milton x Early McIntosh	-5.70
Milton x Ruby Gem	-2.81
Milton x Carrington Red	1.48
Milton x Williams Favourite	1.62
Early McIntosh x Milton	-0.16
Early McIntosh x Carrington Red	0.07
Early McIntosh x Sayers	7.22
William's Favourite x Early McIntosh	-3.08
William's Favourite x Sayers	-3.31
William's Favourite x Golden Delicious	5.56
Jonathan x Stark's Earliest	4.21
Jonathan x Milton	1.47
Jonathan x Early McIntosh	1.61
Jonathan x Canterbury	3.72
Jonathan x Ruby Gem	3.12
Jonathan x Carrington Red	0.99
Jonathan x Stark Earliblaze	-10.85
Jonathan x Sayers	-2.24
Jonathan x Golden Delicious	-1.59
Delicious x Stark's Earliest	-5.93
Delicious x Milton	2.85
Delicious x Early McIntosh	-1.28
Delicious x Canterbury	-5.10
Delicious x Ruby Gem	-0.36
Delicious x Carrington Red	0.23
Delicious x William's Favourite	-1.83
Delicious x Stark Earliblaze	9.68
Delicious x Jonathan	2.41
Delicious x Sayers	-1.57
Delicious x Golden Delicious	0.67
Delicious x Granny Smith	1.69
Golden Delicious x Early McIntosh	-1.59
Golden Delicious x Carrington Red	-1.51
Golden Delicious x Jonathan	0.02
Granny Smith x Early McIntosh	1.92
Granny Smith x Sayers	0.32

²SCA expressed as ripening date relative to 'Jonathan'.

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