Genetic Analysis of Japanese Persimmon Fruit Weight

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Abstract. The expected proportion of individuals in progeny having genotypic values for fruit weight over a given selection criterion to the total individuals derived from a cross was estimated by multiple-regression analysis in which inbreeding coefficient (F) and midparental (MP) value were independent variables and progeny mean was the dependent variable in Japanese persimmon (*Diospyros kaki* Thunb.). A total of 117 seedlings from 39 crosses was used. Genetic differences of progenies among crosses could be explained solely by F and MP, the effect of the former being greater than the latter. The expected proportion of progenies with large fruit decreased as MP decreased and severely decreased as F increased. Based on the parental mean of 35 fruit on a single tree for 3 years, the proportion of individuals in progeny with fruit weight >200 g was estimated as 34%, 21%, and 12% for 0, 0.125, and 0.25 F values, respectively, in individual from a cross with MP = 200 g.

In the genetic analysis of quantitative characters in fruit breeding, estimating heritability has been one of the major subjects (Bell and Janick, 1990; Caldwell and Moore, 1982; Fanizza and Raddi, 1973; Firoozabady and Olmo, 1982; Hansche et al., 1968, 1972a, 1972b; Kester et al., 1977; Machida and Kozaki, 1975). The heritability usually reported is the narrow-sense heritability [estimated by coefficient of regression of progeny means on midparental (MP) values], which is frequently used in animal breeding (Falconer, 1989). Narrow-sense heritability is, by definition, a proportion due to average effects of genes or additive gene effects among total variation and a measure of the degree to which we can predict the genotypic mean of progenies from their parental phenotypes. Heritability is useful for predicting the response to selection, i.e., the difference in the mean phenotypic value between the progenies of the selected parents and the whole parental population before selection. Genetic improvement can be well advanced in traits with high heritability.

High heritabilities have been obtained for many fruit traits, and selection based solely on parental phenotypes has been effective for getting desirable progenies (Hansche, 1983).

Once a single superior individual has been selected in fruit breeding, it can be propagated and planted as a promising cultivar, whereas in animal breeding the objective is to improve the population as a whole because asexual propagation is impossible. Selection in fruit breeding is based exclusively on individual selection in the F_1 generation. In selection, the variance of the trait to be improved and population mean are important. However, the concept of the heritability developed in animal breeding includes only the average effect of genes, not the variance. The genetics that can be effectively used in fruit breeding should be different from those used in animal breeding.

Fruit breeders are eager to know the expected proportion,

without environmental bias, of individuals in progeny over a given selection criterion in a cross. This proportion provides information on the number of individuals required for a breeder to grow the cross.

Generally, random mating among parents, an assumption required for estimating the narrow-sense heritability and response of selection, is rarely satisfied in practical fruit breeding. First, many fruit traits have a high narrow-sense heritability, so individual selection is effective and breeders are likely to repeatedly use superior cultivars and selections as parents. 'Fuyu' Japanese persimmon and 'Nijisseiki' Japanese pear (Kajiura and Sato, 1990) are such examples. Thus, crosses are not limited to individuals in the next generation, but often include genotypes in the parental population, although it is necessary to compare successive generations to describe the change of the genetic properties from one generation to the next (Falconer, 1989). Therefore, the response to selection over several generations can hardly be predicted. Second, the size of the parental population in which crossings are made is restricted.

Japanese persimmon breeding at the Fruit Tree Research Station (FTRS) at Okitsu, Japan, started in 1938 from crossings among a small number of late-ripening pollination-constant, nonastringent (PCNA) cultivars (Kitagawa and Glucina, 1984; Yamada, 1993) and has continued on a small scale with the main goal of releasing early ripening PCNA cultivars (Yamada, 1993). That situation has resulted in the inbred persimmon population we have.

Large persimmons are commercially attractive in Japan. A breeding target at FTRS is 200 g or higher in fruit weight for genotypes that ripen in October and 250 g or higher for those that ripen in November.

The purpose of this study was to elucidate the effect of inbreeding and midparental value of a cross on fruit weight of progenies and to estimate the proportion of individuals exceeding selection criteria in a cross, without environmental bias.

Materials and Methods

The population. Our study was based on the breeding records of the FTRS Japanese persimmon program at Akitsu and used data on three individuals in a progeny from each of 39 crosses, measured

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from 1982 through 1985. The crosses were made solely for the purpose of genetic improvement without any regard to a specific mating design. One scion was taken from each seedling and top-grafted on branches of mature 'Fuyu' trees (one scion per branch) to promote early fruiting. This population was slightly inbred. Although Japanese persimmon is hexaploid (Zhuang et al., 1990), the genomic composition has not been elucidated. The inbreeding coefficient (F), tentatively calculated as diploid, was 0 in twenty-five crosses, 0 to 0.2 in four crosses, 0.2 to 0.3 in nine crosses, and 0.5 in one cross.

The parents consisted of PCNA cultivars and selections except for 'Nishimurawase', a pollination-variant nonstringent (PVNA) type (Kitagawa and Glucina, 1984; Yamada, 1993).

Evaluating fruit weight. Data on individuals in progeny were collected for 1 year from 1982 to 1985, although parents were evaluated for 3 years from 1984 to 1986 based on 35 fruit per year on a single tree. The weight of five fruit was measured for each individual. Since there was a correlation between mean and standard deviation, data were logarithmically transformed before statistical analysis (Yamada et al., 1993b) so that no correlation occurred. Data were adjusted for yearly variation by subtracting the yearly deviation of the average performance of 19 genotypes using 15 fruit on a single tree of each in the same way as reported by Hansche and Brooks (1965).

Estimating genetic parameters. The multiple-regression analyses were carried out using progeny mean in a cross as a dependent variable and MP and F as independent variables.

In the following description, progeny mean and offspring refer to the mean value in a cross and the value of individuals of progeny, respectively. The analysis revealed the variance due to the multiple regression (σ_r^2). Coefficients of determination were calculated.

Also, an analysis of variance for data of each offspring was made to divide the total variance into between-cross variance (σ_{b1}^2) and within-cross variance (σ_w^2). The σ_{b1}^2 consists of σ_r^2 and the variance that cannot be explained by the regression (σ_{b2}^2); σ_{b2}^2 was calculated by subtracting σ_r^2 from σ_{b1}^2 .

Fig. 1. Relationship between crossing year and deviation of progeny mean in the cross from the multiple-regression line.

The σ_w^2 consisted of genetic and environmental variance, σ_e^2 , which was estimated from measurements of five fruit on a single tree in a single year after the yearly adjustment. It was estimated as $(\sigma_f^2/5) + \sigma_t^2 + \sigma_{gy}^2 + \sigma_{ty}^2 + \sigma_e^2$, where σ_f^2 is the variance among fruit within a tree, σ_t^2 is the variance among trees, σ_{gy}^2 is the variance due to the genotype $\times$ year interaction, and σ_{ty}^2 is the variance due to the tree $\times$ year interaction. An estimate of the error variance due to the adjustment for yearly variation is σ_e^2 , which was estimated as $(\sigma_f^2/15 + \sigma_{ty}^2 + \sigma_{gy}^2)/19$, the variance of the yearly mean of 19 control genotypes (Snedecor and Cochran, 1972). Diverse estimates of environmental variance components were previously obtained (Yamada et al., 1993b).

Within-cross genetic variance (σ_{wg}^2) was calculated by subtracting σ_e^2 from σ_w^2 . Taken together, σ_{wg}^2 and σ_{b2}^2 constitute the genetic variance derived from the deviation from the regression line toward MP values. The environmental variance included in MP values (σ_{MPE}^2) was estimated as $[(\sigma_f^2/35 + \sigma_{gy}^2 + \sigma_{ty}^2 + \sigma_e^2)/3 + \sigma_t^2]/2$.

The uniformity of within-cross variance was tested by Bartlett's test (Snedecor and Cochran, 1972). It was not significantly rejected at $P = 0.05$.

The deviation of the value in each progeny mean from the multiple regression line was tested for the normality of the distribution by Kolmogorov-Smirnov's one-sample test (Campbell, 1974), and the normality was not rejected at $P = 0.05$.

Results

Mean fruit weight for MP value and progeny mean were 2.326 (log 212 g) and 2.246 (log 176 g), respectively. No relationship was found between the deviation of progeny mean of each cross from the multiple-regression line and the year of crossing (Fig. 1).

As the result of the multiple-regression analysis, partial regression coefficients of -0.2881 ± 0.0822 for F and 0.2842 ± 0.2068 for MP were obtained. The analysis yielded the following equation:

$$Y = 1.6075 - 0.2881 F + 0.2842 MP$$

where Y is the estimated progeny mean in the cross.

F test showed the significance at $P = 0.01$ for the effect of the multiple regression (Table 1). The coefficient of determination was 0.34. Partial regression coefficients were significant at $P = 0.01$ for F and nonsignificant at $P = 0.05$ for MP. Standardized partial regression coefficients were -0.50 for F and 0.19 for MP. The coefficient of determination in the multiple regression (0.34) was higher than one in the regression of only F (0.25). No significant correlation was found between F and MP.

The analysis showed that F had a greater influence on Y than MP. The regression of MP after removing F was nonsignificant at $P = 0.05$ (Table 1). Selecting a parental combination with a fairly large MP alone can hardly be expected to yield progenies having large fruit (Fig. 2). For example, it was estimated that progenies from parents having an MP of 300 g would provide the mean of 205 and 174 g in case of 0 and 0.25 of F, respectively.

As the result of the analysis of variance (Table 1), between-cross variance (σ_{b1}^2) was estimated as very small compared to within-cross variance (σ_w^2). The σ_{b1}^2 and σ_{b2}^2 values were estimated as 8.763×10^{-3} and 0.056×10^{-3} , respectively (Table 2), a result suggesting that the genetic differences among crosses due to factors other than F and MP were very small. The F test for the null hypothesis of $\sigma_{b1}^2 = \sigma_r^2$ was not significant at $P = 0.05$. Neglecting σ_{b2}^2 , σ_{wg}^2 was considered the only genetic variance derived from the deviation from the multiple-regression line. Genetic variances

Table 1. Analysis of variance for Japanese persimmons weight using 117 offspring from 39 crosses.

Sources of variation	df	Sum of squares ^z	Mean squares ^z	F test	Expected mean squares ^y
Between cross	38	610.91	16.077	1.47 ^{NS}	$\sigma_B^2 = \sigma^2 + (2/38) \sigma_R^2 = \sigma_w^2 + 3\sigma_{bl}^2 = \sigma_w^2 + 3\sigma_r^2 + 3\sigma_{b2}^2$
Regression ^x	2	210.12	105.060	9.44 ^{**}	$\sigma^2 + \sigma_R^2$
Only F	1	189.15			
MP ^w after removing F	1	20.97	20.970	1.88 ^{NS}	
Only MP	1	72.84			
F after removing MP	1	137.28	137.280	12.33 ^{**}	
Residual	36	400.79	11.133		$\sigma^2 = \sigma_w^2 + 3\sigma_{b2}^2$
Within cross	78	855.18	10.964		σ_w^2
Total	116	1466.09	12.639		$\sigma_w^2 = (114/116) \sigma_{bl}^2$

^zLogarithmically transformed value, multiplied by 10⁻³.
^y $\sigma^2 = \sigma_w^2 + 3\sigma_{b2}^2$, $(2/38) \times \sigma_R^2 = 3\sigma_r^2$, $\sigma_{bl}^2 = \sigma_r^2 + \sigma_{b2}^2$. See Table 2 for variance components.
^xMultiple regression of progeny mean in a cross to F and midparental value. F = inbreeding coefficient.
^wMP = midparental value.
^{NS, **}Nonsignificant at *P* = 0.05 or significant at *P* = 0.01.

Fig. 2. Progeny mean estimated by the multiple regression of inbreeding coefficient and midparental value based the parental mean performance in measurements repeated for 3 years using 35 fruit from a single tree. Vertical bars = SE of the estimates when F = 0.

were estimated as 2.220×10^{-3} for the MP value and 8.763×10^{-3} for the progeny population.

The environmental variance of MP (σ_{MPE}^2) was estimated at 0.293×10^{-3} , which was only 3.3% of σ_{wg}^2 . Offspring in a cross were assumed to be normally distributed around the estimated value on the regression line with the variance of σ_{wg}^2 .

Figure 3 indicates the expected proportion of offspring with a genotypic value higher than a critical value, as predicted from the mean performance in parents, which was determined for 3 years using 35 fruit samples on a single tree.

The expected proportion of offspring with large fruit decreased as MP decreased or F increased, the degree of change being greater with a change of F. Crosses with higher MP values cannot be expected to yield offspring having a high proportion of large fruit, even at F = 0. The probability of obtaining offspring of 200 g or higher was estimated to be 34%, 21%, and 12% for 0, 0.125, and 0.25 F values, respectively, when MP was 200 g. The probability

Table 2. Estimates of variance components obtained from the analysis of variance of Japanese persimmon fruit weight using 117 progenies in 39 crosses.

Variance components	Estimates ^z
Between cross (σ_{bl}^2)	1.704
Regression ^y (σ_r^2)	1.648
Residue (σ_{b2}^2)	0.056
Within cross (σ_w^2)	10.964
Genetic (σ_{wg}^2)	8.763
Environmental ^x (σ_e^2)	2.201
Total (σ_t^2)	12.668

^zLogarithmically transformed value multiplied by 10⁻³.
^yMultiple regression of progeny mean in a cross on inbreeding coefficient and midparental value.
^xVariance computed from estimates of variance components in our previous reports (Yamada et al., 1993b). Offspring performance based on the measurement for five fruit on a single tree without yearly repeating as follows: $\sigma_e^2 = \sigma_f^2/5 + \sigma_t^2 + \sigma_{gy}^2 + \sigma_{ty}^2 + \sigma_e^2$, where σ_f^2 is within-tree variance, σ_t^2 is between-tree variance, σ_{gy}^2 is the genotype $\times$ year interaction variance, σ_{ty}^2 is the tree $\times$ year interaction variance, and σ_e^2 is the error variance due to the adjustment for yearly variation

of obtaining fruit 250 g or higher was 7%, 3%, and 1% for 0, 0.125, and 0.25 F values.

Discussion

Multiple regression analysis indicates that most between-cross variance can be explained by a linear combination of F and MP. This implies that the genetic differences among crosses were influenced little by unknown factors. The coefficient of determination in the multiple regression (0.34) was higher than in the regression to F (0.25), suggesting that the former is more effective than the latter, although the effect of MP is small.

The deviation of each progeny from the multiple-regression line was solely due to the segregation within crosses. The expected proportion of offspring with fruit weight equal to or above the selection criterion can be easily computed when the uniformity of within-cross variance and the normality of within-cross distribution is satisfied. Bartlett's test and Kolmogorov-Smirnov's one-sample test did not reject the assumption at *P* = 0.05 for the uniformity of within-cross variance among crosses and the normality of the distribution within cross in progeny, respectively.

It was found that fruit weight was greatly affected by inbreed-

Fig. 3. Proportion of offspring having genotypic values of >150 g (A), 200 g (B), and 250 g (C), respectively, predicted by the multiple regression based on parental performance in measurements repeated for 3 years using 35 fruit each year from a single tree. Solid line, $F = 0$; broken line, $F = 0.125$; and dashed line, $F = 0.25$. Vertical bars = the range of the expected proportion for $F = 0$ in $\pm \text{SE}$ points of cross mean predicted by the multiple-regression analysis, assuming the estimates of diverse variance components are valid.

ing, but, even when F was equal to 0, the mean of progenies was smaller than that of the parents. There are several possible causes for this. First, this may result from juvenility, as was shown in peach (Kanato et al., 1980; Yoshida et al., 1984). Top-grafting has been used in persimmon breeding at Akitsu, one purpose being to make progenies show the same characteristics as the adult, even at an early stage after the start of fruiting. No correlation was found, however, between the deviation from the multiple-regression line and the years after crossing, a result indicating that fruit did not become larger with the passing of years after grafting. Moreover, Yamada and Kurihara (1984) found a similar trend in 50 and 79 offspring bearing fruit for several consecutive years. Therefore, juvenility did not seem to reduce progeny fruit weight.

Second, even crosses in the $F = 0$ might not actually be noninbred, because the ancestry of every parent here is unknown. It is possible that inbreeding, to a greater or lesser extent, might have been involved in the initial population. All parents used here and resulting selections were of the PCNA type except for 'Nishimurawase'. All nonastringent cultivars are of Japanese origin, except for 'Luo Tian Tian Shi', which is of Chinese origin (Yamada et al., 1993a; Wang, 1982). Two groups, PCNA and PVNA, are included among the nonastringent cultivars. The number of PCNA native cultivars is limited, and they have narrow variation with distinctive features different from other groups (Yamada et al., 1993a). Their origin is restricted to the central districts of Japan. Their fruit are flat, while in other groups fruit range broadly from flat to oblong.

Moreover, PCNA native cultivars are mostly late ripening.

Many PCNA cultivars have fruit that have cracks, which are infrequent in the other types (Yamada et al., 1988). Kikuchi (1948) mentioned that the PCNA cultivar first appears in the literature in the seventeenth century, while PVNA is found in thirteenth century writing and the astringent type in the tenth century, an indication that PCNA is of the most recent origin (Yamada, 1993).

PCNA's distinctive variability also suggests the recent origin of PCNA cultivars. Moreover, the PCNA genotype is recessive to the others (Ikeda et al., 1985). Therefore, it is deduced that PCNA native cultivars might have been derived from natural crossings among closely related cultivars. This suggests that some degree of inbreeding was involved in the formation of the original population of PCNA cultivars. This may explain the fact that progeny means were smaller than MP values, even in crossings with $F = 0$. In practical breeding, it is important to avoid inbreeding and yet to try to detect crosses that show heterosis among crosses with $F = 0$.

Persimmon cultivars have been improved mostly with the aim of producing early ripening PCNA cultivars with good fruit quality. Most crosses between PCNA and other types yielded no PCNA offspring (Ikeda et al., 1985). Therefore, crosses among late-ripening PCNA cultivars, and between them and the resulting PCNA selection, were carried out. Although breeding on a small scale with a limited number of parents improved the date of fruit ripening, a trait on which inbreeding had little or no influence (Yamada 1993), it was difficult to obtain promising genotypes with high fruit weight. Fruit breeders should make their crosses among parents with broad genetic variability, although it might make cultivar improvement slower for characters on which in-

breeding has little influence. It seems to us that fruit breeders generally make crosses to obtain a promising cultivar hastily, in only a single generation. This inevitably results in inbreeding depression for several characters.

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