Combining Ability Analysis of Juvenile Period in Pear

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Abstract. Combining ability for transmission of juvenile period duration was studied in a large pear breeding population. The 92 parents, consisting of cultivars and selections of *Pyrus communis* L. and its interspecific hybrids with *P. pyrifolia* (Burm.) Nakai and *P. ussuriensis* Maxim., as well as genotypes of *P. calleryana* Decne., were crossed in 298 combinations. General combining ability was highly significant and of much larger magnitude than specific combining ability, indicating that juvenile period length was under predominantly additive genetic control. Selection of parents based on their juvenile period or their combining ability constants is likely to result in significant reduction in mean juvenile period.

The length of the juvenile period is a major impediment to rapid progress in tree fruit breeding (Hansche and Beres, 1980). In pears, typically, a minimum of 4 years of growth is needed before seedlings flower, although juvenile periods are frequently much longer (Visser, 1964, 1967, 1976; Visser et al., 1976; Zimmerman, 1976, 1977). The juvenile period of pear seedlings has been shown to be positively correlated with their precocity as clonal trees propagated from physiologically adult tissue (Visser and De Vries, 1970). Therefore, in addition to shortening the generational time, selection of seedlings with short juvenile periods may indirectly select for precocious bearing.

The juvenile period in pears is inherited quantitatively, with significant differences among parents in their ability to transmit short juvenile periods to their offspring (Dept. of Horticulture, Chekiang Agricultural Univ., 1978; Visser, 1976; Zielinski, 1963; Zimmerman, 1976). In an analysis of a partial diallel cross of 12 *Pyrus communis* cultivars, Visser (1976) found general combining ability to be significant, while specific combining ability was not, and concluded that the mode of gene action for this trait was largely additive.

Zimmerman (1976) estimated the combining ability of 20 cultivars and selections using a non-least squares estimation of half-sib family means from an incomplete diallel. Although certain progenies were common to

both studies, the present analysis provides least-squares estimates of general combining ability for more parents. Our objective was to estimate the relative importance of general (GCA) and specific combining ability (SCA) to the inheritance of juvenile period in pear and to use the results to improve breeding efficiency.

The base population for study consisted of seedling progenies planted at the Agricultural Research Station, Beltsville, Md., from 1964 to 1971. The seeds were germinated in January-February, and the seedlings were planted in the orchards in May of each year. Progenies planted through 1968 have been described previously (Zimmerman, 1976, 1977). In contrast to these studies, seedlings planted in 1962 and 1963 were deleted from the data set because differences in first-year management practices, specifically planting date, appeared to significantly lengthen their juvenile period in comparison with subsequent progenies of identical parentage. In addition, part of the 1968 and 1969 plantings were deleted because of poor growth, presumably due to waterlogging in their orchard site. Seedlings that died or were otherwise eliminated before flowering were not included in the data set. Flowering data were collected each spring, as described by Zimmerman (1976, 1977). Tree age in the first

year in which flowering was observed was equated with the length of the juvenile period. Seedlings were evaluated for a minimum of 8 years and a maximum of 10 years. In plantings evaluated for longer periods, data on seedlings that flowered after 8 years were also deleted from the data set to eliminate bias due to unequal evaluation periods. Only 13% of all seedlings were excluded by this restriction.

All progenies of parents not involved in at least two crosses were also deleted. These restrictions resulted in a population of 8513 seedlings distributed among 298 crosses made among 92 parents. Progeny size varied from two to 94 seedlings, with a mean of 28.6 seedlings. Although some crosses were replicated in at least 1 additional year, the set of crosses planted in any given year were predominantly unique. With some exceptions, many parents were involved in crosses in more than 1 year. The parental genotypes consisted of 67 cultivars and selections of *Pyrus communis* L. origin, two genotypes of *P. calleryana* Decne., 10 genotypes of *P. communis* × *P. pyrifolia* (Burm.) Nakai, eight of *P. communis* × *P. ussuriensis* Maxim., two selections of *P. communis* × *P. pyrifolia* × *P. ussuriensis*, and two of uncertain origin.

The analysis of variance of combining ability was computed by a least-squares fitting of constants as outlined by Gilbert (1967). Both parents and crosses were assumed to be fixed effects, and, therefore, F tests of GCA and SCA were computed using within-family residual mean square as the error term. Reciprocal crosses were combined, and only parents involved in at least two crosses were included in the analysis. Parental general combining-ability values computed by the program were adjusted by subtracting half the general population mean.

Significant differences in mean juvenile period (JP) were found among the crosses (Table 1). The shortest mean JP was found in progeny of US 56112-075 × US 56112-146 (3.2 years), while the highest was found in the progeny of 'Moonglow' × 'Winter Cole' (7.2 years). The overall distribution was slightly skewed toward shorter juvenile periods (data not presented). The population mean was 5.1 years. Eighteen individual seedlings from several crosses flowered as early as after 2 years.

GCA was highly significant (Table 1). This is promising in view of the complex physiological nature of juvenility and flowering (Zimmerman, 1972). SCA was also highly significant in this fixed effects analysis, al-

Table 1. Analysis of combining ability for transmission of juvenile period in pear.^z

Source	df	Mean square	F	Probability > F
Crosses	297	18.79	13.14	0.001
GCA	91	46.94	32.83	0.001
SCA	206	6.36	4.45	0.001
Within family residual error	8215	1.43		

^zFixed effects model.

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though the mean square for GCA was more than seven times as large as that computed for SCA. The results suggest that the effects of genetic factors controlling juvenile period are predominantly additive. The significance of SCA effects could be due, in part, to the mating design, an incomplete diallel with multiple missing crosses. The relative significance of GCA and SCA are similar to those reported by Visser (1976).

GCA constants varied from -1.09 for US 58307-037 to 1.48 for 'Virginie Baltet' (Table 2). The number of crosses per parent ranged from two to 29, with 49 parents (16%) in four or fewer crosses. Relative rankings should be interpreted in view of the number of crosses and the standard errors. The species pedigree of a parent did not appear to affect transmittance of juvenile period, the genotype of each individual parent being of more importance. The mating design, the number of parents not of *P. communis* pedigree, and differences in ancestry prevent generalized conclusions of species differences. With the exception of 'Dawn', the rankings of parents as reported in this study are in general agreement with those reported from a smaller set of crosses (Zimmerman, 1976). Of the 14 parents in common, the best five and the worst five previously reported were also grouped closely by GCA. 'Dawn' appeared somewhat lower in rank in the present study.

Considerable variability in juvenile period exists within the breeding population studied. The significance and magnitude of GCA effects, in comparison to SCA, indicates that genetic progress is possible. Selection of parents on the basis of their own juvenile period should be a highly efficient method of shortening the mean juvenile period of this breeding population.

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Table 2. Ranking of 92 parents by combining ability constants (GCA) for juvenile period, standard errors of the constants, number of crosses, and species pedigree.

Parent	Species ^z	No. crosses	GCA ^y	SE
US 58307-037	CP	4	-1.09**	0.09
NJ 501871129	CU	2	-0.96	0.46
NJ 501971211	CU	2	-0.87	0.38
US 56112-075	C	5	-0.73**	0.13
US 56112-119	C	5	-0.73**	0.10
Turkey No. 7	Unk	9	-0.67***	0.10
NJ 5001710820	CU	8	-0.65***	0.08
US 56112-114	C	8	-0.64***	0.09
Bartlett	C	16	-0.58***	0.07
US 725	C	3	-0.57	0.18
NJ 487601092	CPU	12	-0.56***	0.07
Michigan-US 572 4X	C	4	-0.55	0.18
Ananas de Courtrai	C	7	-0.50***	0.10
Kieffer	CP	13	-0.49***	0.05
US 56119-066	C	3	-0.48	0.14
US 309	C	20	-0.47***	0.06
US 56112-036	C	15	-0.44***	0.06
US 386	C	10	-0.41***	0.07
US 56112-146	C	12	-0.37***	0.07
US 56111-020	C	3	-0.31	0.20
Bradford	Ca	11	-0.30***	0.06
Parberton	C	3	-0.29	0.20
Marie Louise	C	9	-0.29*	0.11
US 301	C	11	-0.28**	0.08
US 414	C	2	-0.28	0.21
NJ 501971234	C	9	-0.26*	0.08
NJ 5001480202	CU	6	-0.26	0.13
US 643	CP	11	-0.22*	0.09
Old Home	C	4	-0.20	0.07
Gorham	C	7	-0.19	0.10
US 278	C	5	-0.19	0.11
NJ 490871089	CU	14	-0.17*	0.07
US 342	C	18	-0.17*	0.06
Hansen's Seedling	U	3	-0.16	0.21
Beurre d'Anjou	C	2	-0.13	0.23
US 337	C	16	-0.11	0.06
Magness	C	17	-0.10	0.06
NJ 5008710504	CU	10	-0.07	0.10
Ottawa 291	C	5	-0.06	0.11
US 264	C	9	-0.06	0.09
US 220	C	3	-0.05	0.20
New Hampshire No. 2	C	7	-0.04	0.09
Roi Charles de Wurtemberg	C	4	-0.04	0.10
US 58320-029	C	4	-0.02	0.15
Tsarigradka	C	3	-0.01	0.10
Colette	C	3	0.05	0.24
US 307	C	10	0.07	0.09
Beurre Bosc	C	2	0.13	0.26
Beurre Dumont	C	4	0.14	0.09
US 571	C	4	0.16	0.15
US 56111-008	CP	3	0.21	0.20
Early Seckel	C	2	0.22	0.19
Doyenne du Comice	C	2	0.25	0.19
NJ 5001480917	CP	3	0.26	0.27
Charles Escaig	C	5	0.27	0.11
Michigan-US 437 4X	C	3	0.28	0.18
US 57207-265	C	2	0.29	0.43
Dawn	C	19	0.29***	0.05
Farmingdale	C	4	0.31	0.16
Moonglow	C	2	0.35*	0.05
Illinois 38	CPU	4	0.38*	0.09
US 539	C	10	0.40***	0.07
Duchesse d'Angouleme	C	3	0.40	0.45
Michigan-US 437	C	3	0.45	0.17
Koonce	CP	2	0.46	0.17
US 56109-043	C	3	0.49	0.17
US 505	C	24	0.49***	0.05
US 446	C	10	0.49***	0.08
<i>P. korshinskyi</i>	C	2	0.57	0.17
Bantam	CU	2	0.57	0.19
US 58303-016	C	3	0.58*	0.13
Ewart	C	12	0.61***	0.06
Bererd	C	3	0.62*	0.11
Russet Winter Nelis	C	2	0.62	0.21

continued

Table 2. *continued*

Parent	Species ^z	No. crosses	GCA ^y	SE
Ayres	CP	4	0.63*	0.10
Stanley	C	2	0.65	0.20
<i>P. calleryana</i>	Ca	2	0.69	0.11
Winter Nelis 4X	C	3	0.70	0.25
US 56111-003	CP	2	0.74	0.17
Packham's Triumph	C	2	0.77	0.26
Maxine	C	29	0.89***	0.08
Winter Cole	C	3	0.90*	0.14
Surecrop	C	3	0.90*	0.10
Missouri 83	C	2	0.92	0.17
Caywood	CP	4	1.08**	0.10
US 57206-221	C	2	1.10	0.45
Golden Spice	CU	5	1.15***	0.12
Beurre Superfin	C	2	1.27	0.60
Starking Delicious	C	4	1.38**	0.11
Tennessee 37S20	CP	2	1.38	0.15
Nebraska City	CUnk	10	1.44**	0.33
Virginie Baltet	C	3	1.48*	0.28

^zSpecies pedigrees: C = *P. communis*, P = *P. pyrifolia*, U = *P. ussuriensis*, Ca = *P. calleryana*, Unk = unknown.

^yNegative and positive GCA values indicate that a parent transmitted juvenile periods shorter and longer, respectively, than the average ($g_i = 0$).

***Significantly different from $H_0: g_i = 0$ at 5%, 1%, and 0.1% levels of probability, respectively.

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