AN ABSTRACT OF THE THESIS OF

Qiang Yao for the degree of Doctor of Philosophy in Horticulture presented on September 30, 1998. Title: Estimation of Genetic Parameters in the Oregon State University Hazelnut (*Corylus avellana* L.) Breeding Population.

Abstract approved: _____
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Heritability in the narrow sense and in the broad sense, variance components and correlation coefficients are important genetic parameters in a breeding program. The estimates of these parameters can provide important information for a breeder in the selection of parents, the most efficient design for evaluation of seedlings and advanced selections and the choice of selection strategy to improve many target traits simultaneously. In addition, histograms showing the distributions of the traits in offspring may provide additional information about parent combinations for the improvement of target traits.

The Oregon State University hazelnut breeding program is developing improved varieties for the kernel market. Estimates of genetic parameters for most traits of interest are not available. Seventy seven trees representing 41 genotypes and 35 progenies were used to investigate midparent values and progeny means for 17 traits, including 13 kernel and nut traits, and 4 phenological traits, for three years.

Estimates for heritability in the narrow sense are all high, ranging from 0.56 for amount of kernel fiber, and 0.58 for date of opening of female flowers to 0.87 for percent

kernel, 0.88 for nut compression index and 0.89 for nut depth. Therefore, progeny means can be predicted from mid-parent values and response to selection is expected to be rapid for the improvement of all traits.

The analysis of variance components revealed that genotypic variance accounted for most of the phenotypic variance. Although significant, the genotype X year interaction only accounted for a very small part of the phenotypic variance. It suggested one year's evaluation of genotypes for all traits should be sufficient except for nut weight, kernel weight, number of nuts per cluster, fiber amount, nut maturity, time of catkin elongation, and time of opening of female flowers.

Genetic and phenotypic correlation coeficients were large and positive for nut size traits (nut length, width, depth, nut weight and kernel weight). Phenological traits (date of opening of female flowers , time of catkin elongation and time of leafing out) were also highly and positively correlated. But most other traits were uncorrelated with each other. Therefore, selection of parents with round nuts of medium size, high % kernel, easily-blanched kernels, and early nut maturity is expected to rapidly improve the population for all of these traits.

Histograms show that all traits have continuous variation. Transgressive segregation is very common. For all traits except blanching ability, parent combinations may be based on midparent values. For the improvement of blanching ability, both parents should blanch easily.

Because existing statistical packages do not allow easy calculation of genetic correlation coefficients for tree fruit and nut crops, the use of a spreadsheet to quickly estimate genetic correlation coefficients is demonstrated.

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Estimation of Genetic Parameters in the Oregon State University Hazelnut (*Corylus avellana* L.) Breeding Population

By

Qiang Yao

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Qiang Yao, Author

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ESTIMATION OF GENETIC PARAMETERS IN THE OREGON STATE UNIVERSITY HAZELNUT (*CORYLUS AVELLANA* L.) BREEDING POPULATION

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

Hazelnut (*Corylus avellana* L.) is a clonally-propagated crop that is monoecious, wind-pollinated, and self-incompatible. The production of hazelnut in the US ranks fourth after almond, walnut and pecan among the nut crops (http://usda.mannlib.cornell.edu/data-sets/crops/9X180/98180/crprnkus.txt). The United States is third in world hazelnut production behind Turkey and Italy, and 99% of the US hazelnut crop is produced in Oregon (Azarenko, 1994). Five to ten % of the world hazelnut crop is sold in-shell, while 90-95% is sold on the kernel market (Mehlenbacher, 1994). To improve target traits, public breeding programs in Oregon, western Europe and Turkey have almost exclusively used the European species to develop new cultivars for areas where *C. avellana* is well-adapted (Mehlenbacher, 1994).

In Oregon, a hazelnut breeding program was initiated in 1969 (Thompson, 1977). Two new varieties have been released. 'Willamette' was released in 1990 (Mehlenbacher et al., 1991), and 'Lewis' was released in 1997 (Mehlenbacher, personal communication). However, 'Barcelona', and 'Ennis' continue to be the two main varieties grown in

Oregon. Other varieties such as 'Casina', and the pollinizers 'Butler', 'Daviana' and 'Hall's Giant' account for a very small part of production. Because the blanching ability of these varieties is very poor, they are not competitive on the blanched kernel market. The famous varieties for the blanched kernel market in the world, such as 'Negret', 'Tonda Gentile delle Langhe' ('TGDL') and 'Tonda di Giffoni', have weaknesses and are not recommended for Oregon. 'Negret' and 'TGDL' are susceptible to big bud mite (*Phytoptus avellanae* Nal. and *Cecidophyopis vermiformis* Nal.), and eastern filbert blight caused by *Anisogramma anomala* (Peck) E. Müller. Although it is highly resistant to big bud mite and eastern filbert blight, 'Tonda di Giffoni' has a high percent of blank nuts and a serious problem with moldy kernels. Therefore, the current objectives of the OSU hazelnut breeding program are to breed varieties for the kernel market, i.e. 1) resistance to big bud mite; 2) round nuts with medium size; 3) high % kernel; 4) precocity and high yield; 5) easily blanched kernels; 6) few nut and kernel defects; 7) early maturity; and 8) free-falling nuts (Mehlenbacher, 1993, 1995). As eastern filbert blight continues to spread in the Willamette Valley, resistance to this fungal pathogen has become increasingly important.

There are many steps in a breeding program, including germplasm collection and evaluation, parent selection and making controlled crosses, seedling evaluation, and advanced selection evaluation. The estimation of genetic parameters, such as heritability, variance components, and correlation coefficients, is important to breeders. They provide important information for breeders in the selection of parents, the choice of an efficient design for evaluation of seedlings and advanced selections and the choice of selection strategy to improve many target traits simultaneously.

The goals of this thesis are to estimate these genetic parameters and discuss the implication of these results for the OSU hazelnut breeding program.

Literature Review

Estimation of narrow sense heritability by parent-offspring regression

Narrow sense heritability is the ratio of additive genetic variance to phenotypic variance (Falconer, 1981). When offspring means are regressed on mid-parent values, the slope of the regression line (regression coefficient) equals $COV(Y, X)/\sigma_x^2$, where Y represents the offspring phenotypic means, and X is the mid-parent values. $COV(Y, X) = (1/2)\sigma_A^2 + (1/4)\sigma_{AA}^2 + (1/8)\sigma_{AAA}^2$ (Becker, 1984). If epitasis is ignored, $COV(Y,X) = (1/2)\sigma_A^2$ and $\sigma_x^2 = Var[(P_1 + P_2)/2]$ (P_1 and P_2 are the two parents) $= (1/4)Var(P_1) + (1/4)Var(P_2) + (1/2)COV(P_1, P_2) = (1/2)Var(P)$ when variance existing in the two parents is assumed to be constant and $COV(P_1, P_2)$ is assumed to be zero. Therefore, $\beta = \sigma_A^2/\sigma_p^2$.

Narrow sense heritability is a measure of the degree to which the performance of progeny can be predicted from that of their parents (Falconer, 1981). It also may provide information for examining major changes in the amount and nature of genetic variability over generations (Hansche et al., 1966). When there is high heritability, performance of progeny can be predicted from mid-parent values, and genetic advance is expected to be rapid (Nyquist, 1981).

Heritability is a function of the breeding population and the conditions under which a specific trait is studied (Falconer, 1981). Different environments, measurement techniques, and statistical procedures can result in different narrow sense heritability

estimates for a trait. The more genetic diversity in the population, the higher the heritability likely will be (Falconer and Mackay, 1996).

Most breeders working with tree fruit and nut crops use existing plantings of seedlings and parent trees to estimate narrow sense heritability, often from a fixed site. Often data is available from many years' observations to estimate heritability in the narrow sense by offspring-parent regression (Hansche et al., 1972a, 1972b; Kester et al., 1977; Mehlenbacher et al., 1993; Thompson and Backer, 1993). However, when Dicenta et al. (1993a, 1993b) estimated heritability in almond based on data from each of three years' observations, the estimates for duration of flowering, density of production, empty nuts and double kernels were highly variable from year to year, due to a variable environmental influence.

To increase narrow sense heritability of a trait, it is necessary to develop precise objective ways to measure the trait and to increase sample size (Hansche et al., 1992a). Because of the time and effort needed to accumulate such data on sufficiently large samples of seedling populations, measurements are seldom as objective as desirable for a heritability study (Scorza et al., 1996). Rating scales for quantitative traits for evaluating large numbers of seedlings in a breeding program should be simple, fast and precise, be comparable at different locations and be independent of different breeding objectives (Thompson et al., 1978). Two general types of data may be gathered: enumeration data on discrete characters and actual measurements on quantitative continuous traits (Scorza et al., 1996; Thompson et al., 1978).

At present, narrow sense heritabilities have been estimated for 22 quantitative traits in hazelnut (Table 1.1). Thompson (1977b) estimated heritabilities for % kernel,

nut weight, fiber amount, kernel shrinkage, nut number per cluster and husk length in 19 progenies, of which 15 had 'Barcelona' as a parent and the others had 'Barcelona' as a grandparent. Except husk length and nut number per cluster, all other traits were highly heritable. A second study showed heritability of big bud mite to also be very high (Thompson, 1977a). A third study showed time of budbreak to also be highly heritable (Thompson et al., 1996). Romisondo et al. (1983) reported their results regarding heritabilities of percent kernel, shell thickness, and kernel volume, and found that all three traits had high heritabilities. Mehlenbacher et al. (1988) investigated heritability of blanching ability and found this trait had moderately high heritability. In a later study, the percentage of good kernels, blanks, moldy kernels, kernels with black tips and doubles were found to be moderately high or high heritability, while shrivelled kernels , poorly filled nuts and brown stain had low heritabilities (Mehlenbacher et al., 1993). Osterbauer et al. (1997) found that three measures of resistance to eastern filbert blight (disease incidence, number of cankers and proportion of wood diseased) had low to moderately high heritability.

These heritabilities were estimated by parent-offspring regression. The regression slope represents heritability in narrow sense. The standard error of the slope indicates the standard error of heritability in the narrow sense. There are three classical parent-offspring regression methods: 1) regression of the phenotypic mean of all offspring from a given biparental combination on the mid-parent (Dicenta et al., 1993a, 1993b); 2) the regression of offspring on mid-parent, in which the mid-parent values are repeated for each of the progeny (Hansche et al., 1972a, 1972b; Thompson et al., 1993); and 3) the

Table 1.1 Narrow sense heritability estimates for hazelnut traits

Trait	h^2	Reference
Black tips	0.60	Mehlenbacher et al., 1993
Blanks	0.51	Mehlenbacher et al., 1993
Brown stain	0.15	Mehlenbacher et al., 1993
Double (twins)	0.84	Mehlenbacher et al., 1993
Good kernels	0.42	Mehlenbacher et al., 1993
Moldy kernels	0.61	Mehlenbacher et al., 1993
Poor fill	0.25	Mehlenbacher et al., 1993
Shrivelled kernels	0.22	Mehlenbacher et al., 1993
Ease of pellicle removal	0.48	Mehlenbacher et al., 1988
Eastern filbert blight		
Disease incidence	0.21	Osterbauer et al., 1997
Number of cankers	0.39	Osterbauer et al., 1997
Proportion of wood diseased	0.47	Osterbauer et al., 1997
Kernel volume	0.57	Romisondo et al., 1983
Percent kernel	0.72	Romisondo et al., 1983
Shell thickness	0.77	Romisondo et al., 1983
Date of budbreak	0.55	Thompson et al., 1996
Big bud mite susceptibility	0.82	Thompson, 1977a
Fiber amount	0.55	Thompson, 1977b
Husk length	0.30	Thompson, 1977b
Kernel shrinkage	0.71	Thompson, 1977b
Number of nuts per cluster	0.10	Thompson, 1977b
Nut weight	0.65	Thompson, 1977b
Percent kernel	0.67	Thompson, 1977b

weighted regression technique of Kempthorne and Tandon (1953). These methods give similar results (Tancred et al., 1995). But (2) gives smaller standard error and (3) is useful if progeny sizes are not equal.

Year-to-year variation in climate can affect traits and thus make it difficult to obtain parental values and progeny means when combining information from many years in a large data set with many missing values. Several studies in tree fruit and nut crops have addressed this situation by adjusting values based on least-square estimates of year effects prior to heritability estimation. This technique has been used in peach (Hansche et al., 1977b), sweet cherry (Hansche et al., 1966), grape (Firoozabady and Olmo, 1987), walnut (Hansche et al., 1972a) and pecan (Thompson and Baker, 1993). In a similar study in almond (Kester et al., 1977), however, the year effect was not significant so unadjusted data were used.

An alternative method can be used for phenological traits which are usually recorded on a calendar date basis (Dicenta et al., 1993; Hansche et al., 1972a, 1972b). Hansche et al. (1972a, 1972b) used a seasonally corrected day unit to minimize the year effect. When Tancred et al. (1995) evaluated heritability of the ripening date of apples, they used days relative to 'Jonathan' to record ripening date of genotypes and this automatically adjusted for seasonal variation. Similarly, Weinberger (1948), and Bailey and Hough (1959) recorded ripening dates of peaches relative to 'Elberta'. Bailey and Hough (1959) presented ripening dates in half-week intervals, while Weinberger used weekly intervals. Phenological traits tend to have high heritabilities in dedicious tree fruit and nut crops regardless of the observational methods used, except peach full bloom date in Hansche's population (Table 1.2).

Table 1.2 Heritabilities of phenological traits in fruit trees and nut crops

Species	Trait	Heritability	Data transformation	Reference
Juglans regia L.	Leaf date	0.96±0.02	Seasonally corrected day unit	Hansche et al.,1972a
	1st shedding of pollen	0.91±0.06	"	"
	Last shedding of pollen	0.68±0.05	"	"
	Receptive date of pistil	0.93±0.02	"	"
	Harvest date	0.85±0.02	"	"
Malus domestica Borkh.	Ripening date	0.92±0.07	Days relative to standard variety	Tancred et al.,1995
Prunus amygdalus Batsch.	First flowering time	0.93±0.06	Uncorrected day unit	Dicenta et al.,1993
	Full flowering time	0.99±0.07	"	"
	Final flowering time	0.84±0.06	"	"
	Duration of flowering	1.05±0.10	"	"
	Time of maturity	0.83±0.08	"	"
	Duration of maturity	0.76±0.08	"	"
Prunus avium L.	1st bloom date	0.65±0.04	Seasonally corrected day unit	Hansche et al.,1966
	Full bloom date	1.00±0.06	"	"
	Ripe date	0.88±0.03	"	"
Prunus persica L.	Date of full bloom	0.78	Uncorrected interval	De Souza et al.,1998a
	Date of ripening	0.94	"	"
	Fruit development period	0.91	"	"
	Full bloom date	0.39	Seasonally corrected day unit	Hansche et al.,1972b
	Ripe date	0.84	"	"
	Short fruit develop-ment period	0.74±0.1	Seasonally corrected interval	Vileila-Morales et al.,1981
	Date of bloom	0.98±0.3	"	"

Although parent-offspring regression may reflect additive genetic action, the method is based on several assumptions (Fehr, 1987): i) the character of interest has Mendelian inheritance; ii) the population is randomly mated; iii) the population is in linkage equilibrium or there is no linkage among loci controlling a character; iv) parents are non-inbred and v) there is no environmental correlation between the performance of parents and offspring. Failure to meet the assumptions can bias the heritability estimates.

Researchers are interested in trying to find methods to reduce the bias of heritability estimates caused by the interaction of genotypes and environments (Casler, 1982; Fernandez, 1985; Byrne et al., 1987). These methods include regressing progeny means from one environment on parent values from a separate environment (Casler and Hovin, 1980b; Vogel et al., 1980). When parents and progeny are evaluated in separate environments, there can be no genotype x environment interaction bias to heritability. Nevertheless, differential environmental expression on parents and progeny can have a drastic effect on the magnitude of heritability estimates (Frey and Horner, 1957). The other method involves estimation and removal of the necessary covariance from the numerator of the heritability estimate, a procedure used by Dudley et al. (1969) to estimate the genotypic covariance between parents and offspring. Casler (1982) believed this kind of covariance analysis between parents and progeny to be the most efficient procedure for estimating heritability for a set of parents and their offspring evaluated together in several replicates or environments using planned designs.

Estimation of variance components and heritabilities

Estimation of variance components may help breeders: i) to carry out efficient experimental designs to distinguish superior from inferior seedlings and allocate resources effectively (Hansche et al., 1972; Marini et al., 1984; Milligan et al., 1990; Trout et al., 1984); ii) to detect magnitude of genotype x environment to recognize what genotypes can perform best under specific environmental conditions (Falconer et al., 1996); iii) to evaluate and estimate different types of heritabilities (Dicenta et al., 1993; Knapp et al., 1987; Singh et al., 1993).

In general, breeders can use different experimental designs and mating systems to analyze variance components and estimate various genetic parameters of interest (Kearsey, 1965). Different experimental designs have different model statements and thus different variance components are estimated.

Dieters et al. (1995) compared ANOVA-based estimates of variance components and variance components estimated by REML. The following three paragraphs come from his review.

"When data are balanced, ANOVA-based estimates of variance components are unique and unbiased, and have the minimum variance among all unbiased quadratic estimators. These optimal statistical properties usually make ANOVA-based estimates the best choice when data are balanced. Although ANOVA-based variance component estimates are derived from sums of squares in the ANOVA table, no assumption of normality is required to derive ANOVA estimators.

"However, for unbalanced data, REML can offer significant advantages over ANOVA-based estimators: REML estimates are unique and nonnegative and have some

useful large sample statistical properties, while ANOVA-based estimates only retain the property of being unbiased. With certain restrictions REML-based estimates are asymptotically normal, consistent and asymptotically efficient as the design size increases. However, these properties have been verified under less restrictive assumptions.

"The derivation of REML estimators requires that an underlying probability distribution for all random effects in the model be assumed. Commonly, a multivariate normal distribution is assumed, even when the data are unbalanced. That REML-based estimators are robust to violations of this assumption has been demonstrated."

Swallow et al. (1984) compared ANOVA, MIVQUE, REML, and ML estimators of variance components for the one-way classification random model with unbalanced data. Their results indicated that the ANOVA estimators performed well, except with seriously unbalanced data when $\sigma_a^2/\sigma_e^2 > 1$; ML was excellent when $\sigma_a^2/\sigma_e^2 < 0.5$, and MIVQUE(A) was adequate; further iteration to the REML estimates was unnecessary. When $\sigma_a^2/\sigma_e^2 > 1$, MIVQUE was poor for estimating σ_a^2 and very poor for σ_e^2, even for just mildly unbalanced data.

Harville (1977) reviewed the literature on the properties, advantages and disadvantages of ML and REML. Briefly, while ML estimates the variance components by those values which maximize the full likelihood function over the parameter space, REML partitions the likelihood into two pieces, one of which is free of the fixed effects, and maximizes only that portion of the likelihood. In contrast to ML, REML takes into account the loss in degrees of freedom associated with estimation of fixed effects.

Knapp et al. (1987) thought planned unbalanced experimental designs might be useful for improving the efficiency of heritability estimation because fewer experimental units were required for degrees of freedom increases with unbalanced relative to balanced designs.

Caro et al. (1985) observed with simulated data that effect of unbalance on variance of heritability might be dependent on estimation methods and data source. The effect of unbalance on variance of heritability was smaller for ML (Maximum Likelihood) than for Method 1, and smaller for heritability based on estimates of sire-plus-dam variance components than for heritability based on estimates of sire or dam variance.

Because of their desirable attributes in providing estimates for variance components for unbalanced data, REML estimates are being used more widely in fruit and nut crops (Tancred et al., 1995; De Souza et al., 1998a, 1998b; Vileila-Morales et al., 1981).

After variance components have been estimated, they can be used to estimate additional genetic parameters of interest. When experimental materials are clonally-propagated varieties and advanced selections, broad sense heritability can be calculated. The estimation of broad sense heritability may be from 3 types of experimental materials: i) among clones for developing an asexually propagated variety (Wricke and Weber, 1986); ii) among homozygous lines for developing a pure line variety (Singh et al., 1993); iii) among experimental hybrids to determine which is superior for releasing as a commercial variety (Gardner, 1961). When experimental materials are self-pollinated species, if there are no non-additive genetic effects, this kind of heritability is called

narrow sense heritability (Rasamivelona, et al., 1995; Gravois, et al., 1991). Because broad sense heritability is defined as ratio of genetic variance to phenotypic variance, the bigger the heritability, the more stable a trait. The trait is more consistent from year to year, location to location, tree to tree, and sample to sample, when there is higher heritability in the broad sense. Therefore, broad sense heritability is a measure of stability of a trait. It may be also used to effectively allocate resources in genotype evaluation (Gravois, et al., 1991; Hansche, et al., 1965; Milligan, et al., 1990; Rasamivelona et al., 1995).

Broad sense heritability usually have two kinds of formulas for phenotypic variance (Fehr, 1987; Wricke and Weber, 1986), one for individual plants and the other for entry means. In individual plant (mass) selection, plants are selected based on the performance in a single environment. The phenotypic variance among individual plants is $\sigma_p^2 = \sigma_w^2 + \sigma_e^2 + \sigma_{gly}^2 + \sigma_{gy}^2 + \sigma_{gl}^2 + \sigma_g^2$, where σ_w^2 = variation among plants within a row or plot, as measured in the experiment, in which each entry (clone, homozygous line, or F_1 progeny) is usually grown. This term (σ_w^2) is totally environmental variation within rows if all plants within a row are genetically identical (clones, homozygous lines). This term contains some genetic as well as environmental variation if the plants within each row are the progeny of non-inbred parents. The other type of selection is based on the mean performance of progenies, homozygous lines, or replicated clones. Phenotypic variance for replicated rows of progenies, clones, or homozygous lines is $\sigma_p^2 = \sigma_w^2/krly + \sigma_e^2/rly + \sigma_{gly}^2/ly + \sigma_{gy}^2/y + \sigma_{gl}^2/l + \sigma_g^2$ if data for estimating variance components were taken on individual plants, or $\sigma_p^2 = \sigma_e^2/rly + \sigma_{gly}^2/ly + \sigma_{gy}^2/y + \sigma_{gl}^2/l + \sigma_g^2$ if data used for the analysis of variance were means of each row. The k, r, l, and y's

are the number of plants/row, replicates, locations, and years, respectively for the experiment. It is obvious that heritability estimated from the latter form is larger than that estimated from the former. As numbers of locations, years and other factors are changed, heritability is changed too.

One of the objectives of breeders is to find the best way to allocate resources to maximize benefits for selection of clones, pure lines and hybrid progenies. Based on estimates of this kind of broad sense heritability, some researchers studied how to allocate resources for evaluation of rough rice, and head rice yields (Gravois et al., 1991), and sugarcane yield components (Milligan et al., 1990), and straighthead in rice (Rasamirelone et al., 1995).

Hansche et al. (1965) used $\sigma_g^2/(\sigma_g^2 + \sigma_{gy}^2/y + \sigma_t^2/yt)$ to calculate heritability in the broad sense for sweet cherry (*Prunus avium* L.). This formula came from the statistical model: $Y_{ijk} = \mu + g_i + y_j + gy_{ij} + t(gy)_{ijk}$ where $i = 1, 2, 3, \ldots, q$; $j = 1, 2, 3, \ldots, r$; and Y_{ijk} stands for the kth tree in the jth year of the ith genotype. The effects postulated in the model stand, successively, for a constant overall mean (μ), random effects contributed by genotype (g_i), by year (y_j), by genotype times year interaction (gy_{ij}) and by effects peculiar to trees $t(gy)_{ijk}$. He estimated heritability for 18 quantitative characters observed in a *Prunus avium* variety collection, computed on the basis of a single observation and on observations in each of 2 years. He concluded that observation over a period of 2 or 3 years would be an effective means of distinguishing superior from inferior seedlings for most of the studied traits. However, it is comparatively expensive because each additional year of evaluation retards the progress of selection. Spatial replication, in so far as it circumvents this delay, is probably less expensive. On the other

hand, results of this study suggested that improvement in experimental technique and experimental design could provide the same increases in precision at less cost.

More recently, researchers working with tree fruit and nut crops have used similar models to estimate variance components in different species, with data coming from observations in a breeding program at a fixed place over a period of many years (Dicenta, 1993a, 1993b; Hansche et al., 1972a, 1972b; Kester et al., 1977; Mehlenbacher et al., 1993; Thompson and Baker, 1993), including almond, walnut, peach, hazelnut, and pecan. One of the objectives is to estimate the magnitude of genotype by year interaction for studied traits so that breeders can decide to how many years to evaluate target traits.

Mehlenbacher et al. (1993) used 54 trees representing 17 genotypes evaluated for 4 years to estimate variance components for nut and kernel defects in hazelnut. These traits included blanks, brown stain, doubles, moldy kernels, black tips, shrivels, poor fill, and good kernels. The statistical model was $Y_{ijkl} = \mu + G_i + T_j(G_i) + Y_k + (GY)_{ik} + [YT(G)]_{ijk} + \varepsilon_{ijkl}$ where Y_{ijkl} was a value from the lth sample from the jth tree of the ith genotype in the kth year, μ was the overall population mean, G_i the effect of genotype, $T_j(G_i)$ the effect of tree within genotype, Y_k the year effect, $(GY)_{ik}$ the genotype by year interaction, $[YT(G)]_{ijk}$ the interaction of tree nested in genotype and year, and ε_{ijkl} sampling error. They found with the exception of brown stain, there appears to be a great deal of genetic variation for the defects studied. Because large G x Y interaction components were detected for blanks, doubles, moldy kernels, black tips and shrivels, it appeared that sampling over a number of years would be necessary to detect differences

among genotypes. Increasing the number of samples per tree would also help, but there would be little advantage in increasing the number of trees per genotype.

However, few breeders working with tree fruit and nut crops have used estimates of variance components to calculate heritability in the broad sense, although Wricke and Weber (1986) described the principles to calculate broad sense heritability by estimates of variance components in different situations. De Souza et al. (1998a, 1998b) used repeatability instead of heritability in the broad sense.

When data come from offspring, additive genetic variance and narrow sense heritability may be estimated. Different experimental designs and different mating systems have different formulas to estimate narrow sense heritability and other components of genetic variance. Now there are a lot of references in this area of study (Dieters et al., 1995; Kearsey, 1965; Knapp et al., 1985; Knapp, 1986; Mullin, et al., 1992; White et al., 1988), most of which deals with annual crops and forest trees. Recently, De Souza et al. (1998a, 1998b) estimated narrow sense heritability based on seedlings of 108 families from crosses among 42 peach cultivars and selections.

Information from progeny can be used to estimate GCA (general combining ability) and SCA (specific combining ability) effects. GCA and SCA effects reflect additive genetic action and non-additive genetic action; high GCA variance and low SCA variance indicate that additive gene effects are important. In tree fruit, an incomplete diallel without reciprocals can be employed to estimate GCA and SCA because many fruit trees are self-incompatible and cross-incompatible. A general model describing the effects of GCA and SCA (Barritt, 1982; Finn et al., 1992; Luby et al., 1986; Tancred et al., 1995) is: $Y_{ijk} = \mu + G_j + G_k + S_{jk} + e_{ijk}$ where Y_{ijk} is the

phenotypic observation for the progeny member of the family jk, μ is the population mean, G_j is the random variable associated with the GCA of the jth female, G_k is the random variable associated with the GCA of the kth male, and S_{jk} is the random variable associated with the SCA of the parents j and k. In addition, BLUP (best linear unbiased prediction) is also employed to predict future performance of parents (Tancred et al., 1995).

Tancred et al. (1995) studied the ripening date of 13 apple varieties used as parents and 36 crosses, and found that the variance component for GCA (237.8) was nearly 10 times the variance component for SCA (25.4), which indicated a strong influence of additive genetic effects on maturity and agreed with the high heritability in the narrow sense estimate (0.92). Barritt (1982) investigated heritability of red raspberry (*Rubus idaeus* L.) fruit firmness determined from 15 parent clones and for 813 seedlings derived from 44 crosses. Analysis of variance of progeny data showed that general combining ability variance was significant and much larger than specific combining ability variance. Of the parent clones, 'Glen Isla', 'Glen Prosen', 'SHRI 6820/41' and 'SHRI 6820/64' had the firmest fruit and, on the basis of progeny analysis, had the highest general combining ability values. Low GCA values were obtained for the parents 'Summer', 'Malling Leo', 'Malling Admiral', 'Taylor', 'Heide' and 'Meeker'.

Lavi et al. (1993) investigated avocado *(Persea americana* Mill.) traits, and estimated the additive and non-additive genetic variance components based on results from between and within crosses/selfs. In all nine traits examined, i.e. anise scent, fruit density, flowering intensity, fruit weight, harvest duration, inflorescence length, seed

size, softening time and tree size, a significant non-additive genetic variance was detected. Additive genetic variance for all traits was low and non-significant.

Dicenta et al. (1993a, 1993b) used 51 or 32 families of almond seedlings to estimate variance components and heritability for 15 traits. Their data were analyzed by years separately or all years combined. Heritability was obtained using the formula: $h^2 = 2\sigma^2_b/(\sigma^2_b + \sigma^2_w)$ where σ^2_b represents the variance between full-sib families and σ^2_w the variance within each family. The heritability so calculated is halfway between heritability in the narrow sense and heritability in the broad sense. They also estimated heritability by regression of progeny means on midparent values. However, their results revealed that heritability by variance components for 10 traits was lower than that by regression. Their explanation was that the calculated estimates of h^2 by variance components were excessively biased, and were not considered representative because of a large year x family interaction.

When heritability is calculated as the ratio of variance components, there are several methods to estimate precision of heritability (Dieters et al., 1995; Knapp, 1985) The distribution of the variances is not known, but the distribution of the ratio of these estimators can be tractable. The ratio of mean squares , 1-H, has an F-distribution, and exact confidence intervals for heritability have been derived, which are not restricted to a specific experimental design (Knapp et al., 1985). The exact confidence interval procedure can be extended from one factor to two factor mating designs. Functions of heritability on a full-sib or half-sib progeny mean basis from nested or factorial mating design parameters are distributed according to the F-distribution (Knapp, 1986). This kind of exact confidence interval can further be extended to heritability for several

mating and experimental designs (Knapp et al., 1987). In Knapp's series of papers regarding exact confidence intervals, many issues were discussed. Interested readers may look into these papers. However, Singh et al. (1993) used sixty four genotypes from three trials evaluated in randomized complete block designs with three replications at three locations to evaluate broad sense heritability and found the distribution of estimates of heritability could be reasonably approximated by the normal distribution.

In cases where confidence intervals are reported, the standard error of h^2 may not be necessary (Dieters et al., 1995) and vice versa. Therefore, Singh et al. (1995) further used data from barley trials evaluated in incomplete block designs at a single environment or several environments to estimate SE of heritability rather than exact confidence intervals. However, heritability was based on the calculation of individual (mass) selection in Singh's two papers. We still don't know what the distributions of heritability based on clones or progeny means are like.

There are several methods to estimate standard errors such as a Taylor series approximation and Dickerson's method (Gravois et al., 1991; Milligan et al., 1990; Rasamivelona et al., 1995; Singh et al., 1993, 1995). In case of studies using data from 148 slash pine full-sib progeny tests, Dickerson's method was found to be slightly more conservative than the Taylor series approximation when estimating the variance of heritability estimates, regardless of test size, age, or the trait. Both the Taylor series and Dickerson approximations compared favorably with an empirical estimate of the variance of heritability estimates (Dieters et al., 1995).

Estimation of correlation coefficients

In a breeding program, correlation coefficients can be of several types, including phenotypic correlation coefficients, genetic correlation coefficients (or genotypic correlation coefficients in some cases), and environmental correlation coefficients. Phenotypic correlation coefficients are not linear combinations of genetic correlation coefficients and environmental correlation coefficients (Searle, 1961).

For characters with low heritabilities, the phenotypic correlation is determined mainly by the environmental correlation, whereas for characters with high heritabilities the genetic correlation is more important in determining the phenotypic correlation (Falconer, 1996). A phenotypic correlation that is lower than the genetic correlation does not imply that a negative environmental correlation is involved. A negative environmental correlation is implied only when the ratio of the phenotypic correlation to the genetic correlation is less than the geometric mean of the heritabilities for the two traits (Searle, 1961).

De Souza et al. (1998a) found that most of the genetic correlations among several peach reproductive traits, flower density, flowers per node, node density, fruit density, fruit set, blind node propensity, were much higher than the corresponding phenotypic correlations. This was expected, in part, because the heritabilities were in the low to intermediate range, which indicated an important environmental contribution to the phenotypic variation (De Souza et al., 1998a).

There is more literature concerning estimates of genetic and phenotypic correlation coefficients rather than environment correlation coefficients which indicates that breeders are more interested in estimates of phenotypic and genetic correlation

coefficients. Phenotypic and genetic correlation coefficients are important in a breeding program because they provide some important information for breeders (Falconer et al., 1996): i) they allow comparison of indirect with direct selection; ii) they allow calculation of correlated response to know how the improvement of one trait will cause simultaneous changes in other traits; iii) to establish selection strategy.

Indirect selection, or selection for a secondary trait to obtain a correlated response in a target trait, has a broad range of applications in plant and animal improvement (Searle, 1965). Indirect selection can be an efficient alternative to direct selection for the target trait when: i) the secondary trait has a superior distribution of genetic and environmental parameters, conferring a greater precision of selection; ii) selection for the secondary trait is more economical; and iii) assessment of the secondary trait can be conducted more quickly, shortening the generation time if the secondary trait has a higher heritability than the first one (Falconer, 1981). Two versions of indirect selection, part-record selection and juvenile-mature correlation, have been widely applied to animal and forestry tree improvement programs, respectively (Shaw, 1989).

De Souza et al. (1998a, 1998b) found that direct selection practiced solely for flower density (in either direction) was expected to have a greater effect on fruit density than direct selection for fruit density. Similarly, direct selection practiced solely for early ripening and short fruit development period was expected to have a greater effect on correlated traits than direct selection for early bloom and large fruit mass in his peach population.

A positive genetic correlation is not desirable when the character of interest is associated with an undesirable character, or when different degrees of expression of two

characters are desired. On the other hand, a negative genetic correlation is not wanted when it involves two desirable characters (De Souza et al., 1998b). In a sweet cherry population, high positive genetic correlations existed among the traits full bloom date, ripe date, fruit firmness and fruit diameter (Hansche et al., 1966). These positive correlations coupled with the high heritabilities of these traits indicate that selection of late blooming parents with large and firm fruit should produce rapid genetic progress among offspring, but that selection of early ripening parents with large and firm fruit may result in less rapid genetic progress in this direction. The large positive genetic correlations within this population are not entirely due to pleiotropy, but result at least in part from linkage among genes affecting these traits. If this is the case, selection of parents with favorable linkage among pertinent genes should greatly enhance the rate of genetic gain (Hansche et al., 1966).

Genetic correlation between two characters may be due to pleiotropy, although linkage disequilibrium is also a cause of correlation, which is transitory. The degree of correlation due to pleiotropy expresses the extent to which two characters are controlled by the same genes, but pleiotropic genes do not necessarily cause an observable correlation (De Souza et al., 1998a).

Non-efficiency may be overcome when the estimated genetic correlations are due mostly to linkage disequilibrium. According to Falconer (1996), however, linkage disequilibrium is more likely to occur when crosses are made among cultivars or lines with divergent origins.

It should be noted that selection changes gene frequencies and consequently the heritabilities of the characters (Falconer et al., 1996). Thus, if only the best performing

individuals are selected in each generation, the total variability in the population is reduced and as a result, the selection response is also decreased. Hence, the predictions for the traits are expected to decrease after each additional generation of selection.

Considering that correlated response is a function of the genetic correlation between the characters involved, and that genetic correlation is a function of gene frequency and is very sensitive to changes in it (Bohren et al., 1966), caution is needed in the interpretation of the correlated response. Genetic correlation, and therefore the correlated response, can change rapidly as a result of selection itself and also due to random genetic drift, the former occurring especially only a few genotypes are saved in each generation of selection (Falconer, 1989). Furthermore, when both genetic correlations and heritabilities are low, the correlated response is usually inconsistent and of low predictability (Bohren et al., 1966; Falconer, 1989; Hill and Leath, 1975). Therefore, before applying the theory of correlated response in practice, the breeder should be aware that it does not always work as expected.

Hansche et al. (1972) observed in walnut that all measures of nut and kernel size were highly correlated; e.g., the correlations of nut weight with nut length, suture, cheek and kernel weight were 0.62, 0.72, 0.78, and 0.82 respectively. They were probably sufficiently high, in fact, to negate the practical value of measuring more than 1 of these traits. They suggested that an improvement in the overall efficiency of this breeding program could be achieved by diverting the resources required to measure nut size and weight to increasing the sample size from which kernel characteristics were estimated; i.e., by utilizing the resources expended to obtain more precise measurements.

Firoozabady et al. (1987) thought breeders should keep in mind the possibility of taking advantage of relations between characters, considering a scheme of selection for more than one character at the same time, or minimizing the negative influence of negative correlations between characters using a suitable index of selection.

Conclusions

The objectives of this thesis are to use germplasm in the OSU hazelnut (*Corylus avellana* L.) breeding program as experimental materials to estimate heritabilities in the narrow sense and in the broad sense, and correlation coefficients, including genetic correlation and phenotypic correlation coefficients. The distribution of traits in 35 crosses is also examined in detail. It is expected that these results will be helpful to breeders in selecting suitable parents, evaluating genotypes effectively, and choosing an appropriate selection strategy for improvement of target traits.

CHAPTER 2

ESTIMATES OF NARROW SENSE HERITABILITY FOR NUT, KERNEL AND PHENOLOGICAL TRAITS IN HAZELNUT

Abstract

The Oregon State University breeding program is developing improved hazelnut (*Corylus avellana* L.) cultivars for the kernel market. Most traits of interest are quantitative, yet there is little information available on their heritability. In this study, the heritability of 13 morphological and 4 phenological traits was estimated by regression of offspring means on midparent values. We tested seedlings from 35 crosses among 41 parents made in 1988 and 1989. The parents represented the wide genetic diversity used in the breeding program. Estimates were all high, ranging from 0.56 for amount of kernel fiber and 0.58 for time of catkin elongation and date of opening of female flowers to 0.87 for percent kernel, 0.88 for nut compression index and 0.89 for nut depth. Therefore, parents may be selected based on their phenotypic values and response to selection is expected to be rapid.

Introduction

Hazelnut (*Corylus avellana* L.) is an important nut crop, whose production ranks second or third behind that of almond and walnut among nut crops (Mehlenbacher, 1994). The United States is one of the world's important hazelnut producing countries, and 99% of the US hazelnut crop is produced in Oregon (Azarenko, 1994).

In Oregon, a hazelnut breeding program was initiated in 1969 (Thompson, 1977). It is developing new varieties for the kernel market (Mehlenbacher, 1994). The objectives include precocity and high yield, round nut shape, medium nut size, high % kernel, easily blanched kernels, few nut and kernel defects, early maturity and free-falling nuts. Estimates of heritability in the narrow sense of these traits should help us in selecting suitable parents, and in predicting progeny performance and genetic advance.

Parent-offspring regression is often employed to estimate heritability in the narrow sense of traits for fruit trees and nut crops. Using this technique, Thompson (1977) estimated heritability of nut weight, percent kernel, kernel shrinkage, kernel fiber amount, number of nuts per cluster, and husk length in hazelnut. Nineteen progenies were used in her study, 15 of which had 'Barcelona' as a parent and the other had 'Barcelona' as a grandparent. Thus the genetic base of the population was very narrow. Except for husk length and number of nuts per cluster, all other traits were

highly heritable. Heritability of date of budbreak was estimated later by Thompson et al. (1996) and the value was high (0.55). Mehlenbacher and Smith (1988) evaluated blanching ability, and Mehlenbacher et al. (1993) estimated heritability of good kernels and 7 types of nut and kernel defects, including blanks, moldy kernels, kernels with black tips, doubles, shrivelled kernels, poorly filled nuts and brown stain. They found heritability of the frequency of shrivelled kernels, poorly filled nuts and brown stain was low, but all other traits were moderately to highly heritable.

The objective of this paper was to use part of the existing genetically diverse population in OSU hazelnut breeding program as experimental materials to estimate heritability in the narrow sense of 17 traits related to nut, kernel and phenological traits by parent-offspring regression.

Materials and Methods

Plant materials

Forty-one genotypes were used to estimate parent values (Table 2.1). Two trees were observed for 36 genotypes and the other 5 were represented by a single tree. Spacing of parent trees was 4.8m between rows by 3.6m in rows. The seedlings resulted from 35 controlled crosses involving these 41 parents made in 1988 and 1989. Seedlings were planted 0.9m apart in rows 2.7m apart. For most traits, the observation period lasted two years. Data recorded between August 1994 and March 1995 are

Table 2.1 Parent trees for heritability estimation

Genotype	Origin	Parentage	No. of trees
Aurea	Germany		2
Birk 5-6	USA	014.084 (Barcelona x Daviana) x Negret	2
Brixnut	USA	Prob. Barcelona open pollinated	2
Casina	Spain		2
Contorta	England		2
Daviana	England		2
Fusco Rubra	Germany		2
Gem	USA	Prob. Barcelona open pollinated	2
GH 88-14	France	Cosford x Segorbe	1
GH 140-004	France	Gironell x Negret	2
Hall's Giant	German		2
Mortarella	S. Italy		2
Negret	Spain		2
Ribet	Spain		2
Romisondo G1	N. Italy	Tonda Romana x Payrone	2
Sant Jaume	Spain		2
Segorbe	Spain		2
Tonda di Giffoni	S. Italy		2
TGDL[z]	N. Italy		2
Tonda Romana	C. Italy		2
VR 17-15	USA	Montebello x Gasaway	2
VR 20-11	USA	(Barcelona x Compton) x Gasaway	2
Willamette	USA	Montebello x Compton	2
23.017	USA	Barcelona x Extra Ghiaghli	2
26.072	Russia	From seeds collected in North Caucasus	2
39.044	USA	Ennis x Hall's Giant	2
54.021	Turkey	From seeds collected on Black Sea Coast	1
54.039	Turkey	From seeds collected on Black Sea Coast	1
55.077	USA	TGDL x Extra Ghiaghli	1
55.129	USA	TGDL x Extra Ghiaghli	2
162.017	USA	Montebello x 054.042(Turkish seedling)	2
166.034	USA	Casina x Butler	2
179.043	USA	Henneman #3 (Spain or France) x 044.114 (Montebello x Compton)	2
183.060	USA	Montebello x 014.084 (Barcelona x Daviana)	2
186.080	USA	F4 (unknown, similar to TGDL) x 041.134 (Montebello x Compton)	2
225.077	USA	TGDL x 042.103 (Montebello x Compton)	2
233.007	USA	013.013 (Barcelona x Lansing) x Henneman #3	1
244.001	USA	017.028 (Barcelona x Tombul Ghiaghli) x Willamette	2
245.094	USA	017.075 (Barcelona x Tombul Ghiaghli) x Willamette	2
246.128	USA	033.113 (Lansing open pollinated) x Willamette	2
255.003	USA	043.098 (Montebello x Compton) x Casina	2

[z] TGDL is short for Tonda Gentile delle Langhe

presented as the first year's data, and notes from August 1995 to April 1996 represent the second year. Some seedlings had not yet begun to bear nuts in the first year, but most progenies were represented by 30 seedlings in the second year. In addition, seedlings in only 29 progenies were investigated for nut and kernel traits in 1994 (Table 2.2), as 6 progenies had very few nuts. All seedlings and most parent trees were located at the OSU Dept. of Horticulture's Smith vegetable research farm in Corvallis, Oregon. A few parent trees were located at the nearby USDA-ARS National Clonal Germplasm Repository.

Nut harvest

Nuts from individual trees were harvested when about 95% of the nuts had fallen to the ground. For the parents, because there was a larger distance between trees, nuts from different trees were easily separated. Almost all nuts of a tree were collected. For seedlings, we paid more attention to avoid mixing of nuts from neighboring trees. The nut crop in 1994 was light. Before nuts began to fall from the trees, branches of some individual trees were tied together to better separate neighboring trees. The nuts were picked from the ground at intervals of 4-5 days and piled under each bearing seedling until 95% of the nuts had fallen. The nuts of neighboring trees were distinguished by examination of nut maturity date, color, shape and size and appearance of the apical scar. The nut crop in 1995 was heavy, and only 1/3 to 1/2 of the nuts from each seedling were

Table 2.2 The number of investigated seedlings for all studied traits

Parents of crosses	Year of cross	Code number	NL	NW	ND	NSI	NCI	DOFF	TCE	LO	NM	%K	NWT	KWT	FA	BA	HL	RHL	NNPC
183.060 x VR 20-11	1888	440	26 (20)	28 (20)	28 (20)	28 (20)	28 (20)	27 (28)	27 (27)	27 (27)	27	26 (20)	26 (20)	28 (20)	28 (20)	28 (20)	27	28	28
Willamette x 054.021	1888	444	28 (26)	28 (26)	28 (26)	28 (26)	28 (26)	28 (28)	28 (28)	28 (28)	28	28 (25)	28 (25)	28 (25)	28 (25)	28 (25)	30	28	30
055.077 X Sant Jeume	1888	445	25 (24)	25 (24)	25 (24)	25 (24)	25 (24)	28 (28)	28 (28)	28 (28)	28	27 (23)	27 (23)	27 (23)	27 (23)	27 (23)	28	25	28
188.080 x VR 17-15	1888	448	24 (24)	24 (24)	24 (24)	24 (24)	24 (24)	26 (26)	28 (28)	28 (28)	27	24 (24)	24 (24)	24 (24)	24 (24)	24 (24)	27	24	25
Fusco Rubre X Hell's Giant	1888	4510	22 (18)	22 (18)	22 (18)	22 (18)	22 (18)	23 (23)	25 (23)	24(24)	24	22 (18)	22 (18)	22 (18)	22 (18)	22 (18)	24	22	24
Fusco Rubra x Romisondo G1	1988	4511	28 (20)	28 (20)	28 (20)	28 (20)	28 (20)	25 (27)	28 (27)	27 (27)	28	27 (20)	27 (20)	27 (20)	27 (20)	27 (20)	28	28	28
Fusco Rubra x Casina	1888	4512	28 (24)	28 (24)	28 (24)	28 (24)	28 (24)	26 (28)	28 (28)	28 (28)	28	28 (24)	28 (24)	28 (24)	28 (24)	28 (24)	28	28	28
Contorta x Aurea	1888	453	18	18	18	18	18	28 (21)	28 (23)	28 (28)	20	18	18	18	18	18	23	18	28
Negret x Tonde di Giffoni	1888	454	25 (23)	25 (23)	25 (23)	25 (23)	25 (23)	28 (28)	28 (28)	28 (28)	25	24 (22)	24 (22)	24 (22)	24 (22)	24 (22)	28	25	30
TGDL x Gam	1888	455	30 (18)	30 (18)	30 (18)	30 (18)	30 (18)	31 (28)	31 (28)	31(28)	31	30 (18)	30 (18)	30 (19)	30 (18)	30 (18)	28	28	31
Willemette x Segorbe	1888	4560	28 (22)	28 (22)	28 (22)	28 (22)	28 (22)	30 (28)	30 (28)	30 (28)	28	28 (21)	28 (21)	28 (21)	28 (21)	28 (21)	30	28	30
Negret x 225.077	1888	4561	30 (17)	30 (17)	30 (17)	30 (17)	30 (17)	30 (30)	30 (30)	30 (30)	30	30 (17)	30 (17)	30 (17)	30 (17)	30 (17)	30	30	30
Ribet x Willamette	1888	457	27 (22)	27 (22)	27 (22)	27 (22)	27 (22)	31 (31)	31 (31)	30 (30)	28	27 (21)	27 (21)	27 (21)	27 (21)	27 (21)	30	28	30
TGDL x 054.038	1888	456	30	30	30	30	30	31 (31)	31 (31)	30 (30)	30	30	30	30	30	30	30	30	30
023.017 x GH 088.014	1888	463	30 (25)	30 (25)	30 (25)	30 (25)	30 (25)	31 (31)	31 (31)	30 (30)	30	30 (24)	30 (24)	30 (24)	30 (24)	30 (24)	30	30	30
Willemette x Hall's Giant	1888	4650	28 (28)	28 (28)	28 (28)	28 (28)	28 (28)	30 (30)	30 (30)	30 (30)	30	28 (28)	28 (28)	28 (28)	28 (28)	28 (28)	30	28	30
188.034 x Hall's Giant	1888	4651	28 (28)	28 (28)	28 (28)	28 (28)	28 (28)	30 (30)	30 (30)	30 (30)	30	28 (28)	28 (28)	28 (28)	28 (28)	28 (28)	30	28	30
Cesine x Mortarelle	1889	468	21 (11)	21 (11)	21 (11)	21 (11)	21 (11)	30 (30)	30 (30)	30 (30)	21	21 (11)	21 (11)	21 (11)	21 (11)	21 (11)	23	20	22
Romisondo G1 x 055.128	1888	4710	31 (18)	31 (18)	31 (18)	31 (18)	31 (18)	30 (30)	30 (30)	30 (30)	30	30 (14)	30 (14)	30 (14)	30 (14)	30 (14)	30	30	28
255.003 x 055.128	1888	4711	30	30	30	30	30	30 (30)	30 (30)	30 (30)	30	30	30	30	30	30	30	30	30
Tonda di Giffoni x 178.043	1889	473	27 (22)	27 (22)	27 (22)	27 (22)	27 (22)	31 (31)	31 (31)	31 (31)	27	27 (22)	27 (22)	27 (22)	27 (22)	27 (22)	30	25	28
182.017 x Birk 005-006	1888	475	28 (14)	28 (14)	28 (14)	28 (14)	28 (14)	27 (28)	28 (28)	28 (28)	28	28 (14)	28 (14)	28 (14)	28 (14)	28 (14)	30	28	30
255.003 x Tonde di Giffoni	1888	4760	28 (11)	28 (11)	28 (11)	28 (11)	28 (11)	30 (30)	30 (30)	30 (30)	28	28 (10)	28 (10)	28 (10)	28 (10)	28 (10)	30	27	30
244.001 x Tonda Romana	1888	4781	24 (14)	24 (14)	24 (14)	24 (14)	24 (14)	31 (30)	31 (30)	31 (31)	28	24 (13)	24 (13)	24 (13)	24 (13)	24 (13)	30	24	28
245.094 x Negret	1888	480	28 (13)	28 (13)	28 (13)	28 (13)	28 (13)	29 (28)	28 (28)	28 (28)	28	28 (13)	28 (13)	28 (13)	28 (13)	28 (13)	30	28	30
245.094 x 178.043	1888	481	26 (21)	28 (21)	28 (21)	28 (21)	28 (21)	28 (28)	28 (28)	28 (28)	28	28 (21)	28 (21)	28 (21)	28 (21)	28 (21)	28	28	28
Casina x Brixnut	1888	484	28	28	28	28	28	20 (28)	28 (28)	28 (28)	28	28	28	28	28	28	30	28	30
Ribet x 038.044	1988	485	24 (18)	24 (18)	24 (18)	24 (18)	24 (18)	30 (30)	30 (30)	30 (30)	27	24 (18)	24 (18)	24 (18)	24 (18)	24 (18)	28	24	28
246.128 x Contorte	1888	486	25 (15)	25 (15)	25 (15)	25 (15)	25 (15)	28 (28)	28 (28)	28 (28)	28	25 (15)	25 (15)	25 (15)	25 (15)	25 (15)	28	25	28
23.017 x VR 020-010	1988	488	28 (20)	28 (20)	28 (20)	28 (20)	28 (20)	28 (29)	30 (30)	30 (30)	28	27 (20)	27 (20)	27 (20)	27 (20)	27 (20)	30	28	28
Willamatta x 026.072	1888	490	28 (17)	28 (17)	28 (17)	28 (17)	28 (17)	30 (30)	30 (28)	30 (30)	30	28 (17)	28 (17)	28 (17)	28 (17)	29 (17)	30	28	28
Negrat x Segorbe	1888	5050	30 (11)	30 (11)	30 (11)	30 (11)	30 (11)	30 (30)	30 (30)	30 (30)	30	30 (11)	30 (11)	30 (11)	30 (11)	30 (11)	30	30	30
GH 140.004 x Birk 005.006	1888	5051	26 (8)	26 (8)	28 (9)	28 (9)	28 (9)	28 (30)	28 (30)	27 (30)	27	26 (8)	28 (8)	28 (8)	28 (8)	26 (8)	27	24	28
Negret x 054.038	1888	511	27	27	27	27	27	28 (27)	28 (28)	28 (28)	27	27	27	27	27	27	27	27	27
233.007 x Daviane	1888	520	24	24	24	24	24	22 (23)	22 (20)	22 (23)	21	24	24	24	24	24	24	24	24

[z] Numbers in parentheses represent ones of the first year. Otherwise, they are ones of the second year

harvested. When nuts from neighboring trees were difficult to distinguish, we bound limbs of a tree together and then put mesh bags on every or every other tree in September. After the nuts were harvested, they were dried to about 9% moisture, and stored in a cool room until used.

Observation standards

Nut length, width and depth Nut length (NL) was the distance from the basal to the apical scar. Nut width (NW) was the distance across the nut at its widest point, and nut depth (ND) was the maximum distance from front to back. A 20-nut random sample was used for every parent tree, and a 10-nut sample was used for measurements on seedlings. A digital caliper was used for nut measurements (Mitutoyo Mfg. Co. Ltd., Tokyo, Japan).

Nut shape Two indexes of nut shape were calculated using the nut length, width and depth measurements (Mehlenbacher, 1991b). Nut shape index (NSI) was calculated as the quantity nut width plus nut depth, divided by two times nut length. Nut compression index (NCI) was calculated as the ratio of nut width to nut depth. The shape index is 0.50-0.89 for long nuts, 0.90-1.00 for round nuts, and 1.01-1.30 for oblate nuts, and the compression index is low (around 0.75) for compressed nuts and near 1.0 for round nuts (Mehlenbacher, 1991b).

Nut weight (NWT), kernel weight (KWT) and percent kernel (%K) Two 10-nut samples were weighed for each parent tree. One 10-nut

sample was weighed for each seedling. Only well-filled nuts were used in these determinations. Percent kernel is the ratio of kernel weight to nut weight.

Kernel fiber amount (FB) and blanching ability (BA) The amount of fiber on the kernel pellicle was rated from 1 (none) to 4 (much) and blanching ability was rated from 1 (complete pellicle removal) to 7 (no removal) as described by Thompson et al. (1978). The samples used to calculate % kernel were also used to evaluate FA and BA in the first year. For greater accuracy, two 30-kernel samples were used for parent trees and a 30-kernel sample were used for seedlings in the second year.

Time of leafing out (LO), time of catkin elongation (TCE), date of opening of female flowers (DOFF) and nut maturity (NM) All seedlings and parent trees were observed at 7-day intervals for LO, TCE, and DOFF starting on December 13, 1994 and November 28, 1995. NM was observed at 5-day intervals starting September 5, 1995. Data were recorded as numbers of intervals. LO was recorded as the day when the first leaves emerged and extended from about 50% of the buds of a whole tree. TCE was the day when 50% of the catkins had elongated. The first day when 50% of the pistillate flower stigmas were exserted was recorded as DOFF. NM was estimated to be the day when 95% of the nuts fell off a tree. 'TGDL' was selected as a check variety for TCE and NM, while 'Tonda di Giffoni' was used for LO and DOFF. Phenological traits for check varieties were recorded as 1. If the date for these traits of a tree was

earlier than that of the standard varieties, with intervals of 5 or 7 days, they were given zero or negative scores. Positive numbers more than 1 (2, 3, ...) indicated genotypes later than the standards. If the two trees of the standard varieties developed at different times, the earlier of the two trees was assigned a value of 1.

Number of nuts per cluster (NNPC) Counts of clusters and nuts were performed in August every year before nuts fell. For parent trees, three limbs in different parts of the trees were selected for counts. For seedlings, numbers of nuts and clusters were counted on the whole tree in the first year. In the second year, numbers of nuts and clusters were counted from three branches, each of which bore at least 30 clusters on productive seedlings. Otherwise, numbers were counted on the whole tree.

Husk length (HL) HL was measured as the distance from the bottom to the top of the husk. 10 husks from clusters of 1-3 nuts each were selected at random from every tree and measured for the trait.

Relative husk length (RHL) RHL was calculated as the ratio of husk length to nut length, using the previously calculated average for these two traits for that tree.

The statistical methods

The regression procedure (PROC REG) in SAS program (SAS Institute, 1994) was used to regress progeny means on mid-parent values for each of the 17 traits. Regression lines were fit for each year

separately, and then the slopes were tested for significant difference. When the slopes were not significantly different, a pooled estimate was calculated for heritaility in the two years. Initially, the full model $Y = \beta_{11}X_{11} + \beta_{12}X_{12} + \beta_{21}X_{21} + \beta_{22}X_{22} + \varepsilon$ was used, in which Y values were progeny means, and X_{11} and X_{21} were "dummy" variables to indicate the year. X_{11} was 1 for data from the second year and zero otherwise; X_{21} was 1 for data from the first year and zero otherwise. Similarly, X_{12} was set equal to the mid-parent value in the second year and zero otherwise; X_{22} was set equal to the mid-parent value in the first year and zero otherwise. The 64 progeny means (Y) were regressed on these four predictors. Of these, 35 were from the second year and 29 were from the first year. $Y = \beta_{11}X_{11} + \beta_{21}X_{21} + \beta X + \varepsilon$ was used as the reduced model with a single slope, where Y values were progeny means and X mid-parent means. X11 and X12 had the same meanings as in the full model. β was the common slope of the reduced model when the data were pooled. β_{11} and β_{21} were the two intercepts of the reduced model.

F-statistics was used to test if there was a common slope for the two years' data sets. $F = [(RSSE - FSSE)/1]/(FSSE/n)$, where RSSE = Residual sum of squares for the reduced model, FSSE = Residual sum of squares for the full model, and n = Residual degrees of freedom for the full model. The significance level was set at 0.05.

The slopes of the regression lines provided estimates of heritability, and standard errors of the slopes provided standard errors of these estimates.

Because these heritability estimates might be inflated by genotype x year interaction, 1995 progeny means were regressed on 1994 midparent values and 1994 progeny means were regressed on 1995 midparent values as suggested by Vogel et al. (1980) and this data set was as well used to estimate pooled heritability if there was a common slope for a trait.

To compare the difference in heritability estimates from the two procedures, the data sets used were balanced, i.e. the six progenies for which no data were recorded in the first year were removed from the whole original data set for nut and kernel traits.

Results and Discussion

When we used this technique to estimate heritability of 13 traits with pooled unbalanced data, in which evaluation of parents and offspring was in the same year, all traits were highly heritable (Table 2.3). Estimates were obtained for each of 13 traits in each year but in no case was there a significant difference (Figs. 2.1 and 2.2). For the other four traits, estimates were only available for the second year. They were also highly heritable (Table 2.3). The heritability estimates from the pooled data were between those of the first year and second year, and the standard errors were reduced because of the increased number of data points.

Table 2.3 Heritability of traits in hazelnut by parent-offspring regression method

Trait	2nd Year	1st Year	Pooled
Nut Length	0.67±0.07[z]	0.68±0.07	0.68±0.05
Nut width	0.74±0.07	0.83±0.07	0.78±0.05
Nut depth	0.87±0.07	0.93±0.08	0.89±0.05
Shape index	0.71±0.14	0.58±0.15	0.65±0.10
Compression index	0.89±0.10	0.85±0.12	0.88±0.08
Husk length	0.82±0.07		
Relative husk length	0.91±0.06		
Nut number per cluster	0.67±0.11		
Nut weight	0.64±0.06	0.62±0.05	0.63±0.04
Kernel weight	0.67±0.07	0.67±0.07	0.67±0.05
% Kernel	0.89±0.10	0.85±0.11	0.87±0.07
Fiber amount	0.53±0.14	0.58±0.12	0.56±0.09
Blanching ability	0.62±0.10	0.67±0.11	0.64±0.07
Date of opening of female flowers	0.56±0.06	0.63±0.11	0.58±0.05
Catkin elongation	0.67±0.06	0.70±0.09	0.68±0.05
Leafing out	0.64±0.07	0.76±0.08	0.72±0.05
Nut maturity	0.86±0.11		

[z] Heritability point estimate ± standard error

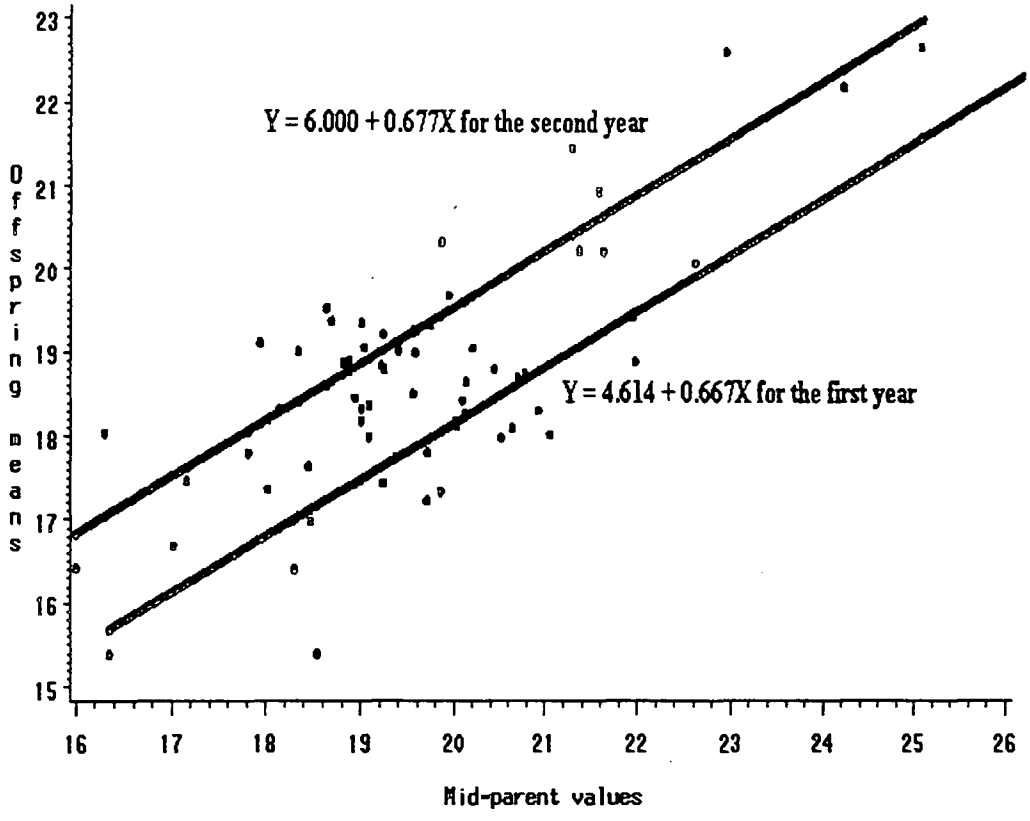

Figure 2.1 Regression of offspring means on mid-parent values for nut length

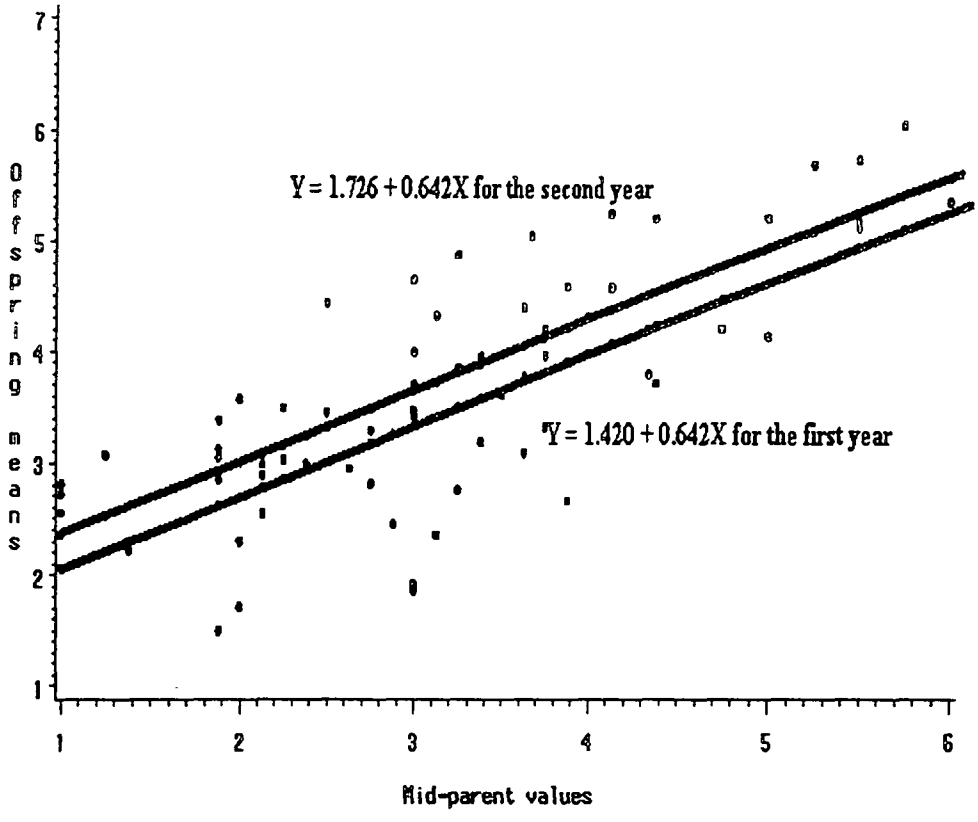

Figure 2.2 Regression of offspring means on mid-parent values for blanching ability

When progeny and parents are evaluated in the same environment, there may be an environmental covariance between parents and progenies, and thus regression may overestimate heritability (Casler, 1982). This bias can be removed by regression of progeny means from one environment on parent values from a separate environment (Casler, 1982). Nevertheless, different environmental expression on parents and progenies might have a large effect on the magnitude of heritability estimates (Vogel et al., 1980). In our case, regression of 1995 progeny means on 1994 midparent values, and of 1994 progeny means on 1995 midparent values produced h^2 estimates that were not significantly different from each other or from the results for the same year's data set for 11 of 13 traits. For DOFF and TCE, however, the results were different from those listed in Table 2.3. When progeny means from 1994 were regressed on midparent values from 1995, the heritability estimates for DOFF and TCE were 0.325±0.049, and 0.386±0.052, respectively. When progeny means from 1995 regressed midparent values from 1994, the heritability estimates for DOFF and TCE were 1.063±0.123 and 1.106±0.109 respectively. When daily average temperatures are lower than 32°F, phenological progress is arrested. This only occurred during January 30, 1996 to February 4, 1996. In the first two weeks of observation period starting Nov. 28, 1995, the temperature was also much higher than in 1994. In the third and second to the last week, the temperature in 1994 was higher than that in 1995. DOFF and TCE are a function of chilling requirements and heat

requirements after chilling requirements are satisfied (Mehlenbacher, 1991a). The temperature change trend resulted in the wider range of values for DOFF and TCE in 1995 than in 1994. Their ranges were from –1 to 13 for DOFF in 1995, from 0 to 11 for TCE in 1995, from 1 to 10 for DOFF in 1994, and from 3 to 10 for TCE in 1994. This might explain why there were no common heritability estimates for these two traits when progeny means from one year were regressed on midparent values from the other.

Year-to-year differences in climate can affect traits and thus make it difficult to obtain parental values and progeny means when combining information from many years in a large data set with many missing values. Several studies in tree fruit and nut crops have addressed this situation by adjusting values based on least-square estimates of year effects prior to heritability estimation. This technique has been used in peach (Hansche et al., 1977b), sweet cherry (Hansche et al., 1966), grape (Firoozabady and Olmo, 1987), walnut (Hansche et al., 1972a) and pecan (Thompson and Baker, 1993). In a similar study in almond (Kester et al., 1977), however, the year effect was not significant so unadjusted data were used. An alternative method for adjusting for year-to-year variation in phenological traits is to express values relative to a standard genotype, as was done by Tancred et al. (1995) for ripening date in apple. In our study, data were collected on parent trees and seedling trees over a 2-year period and used

without adjustment. Phenological traits were expressed relative to standard varieties.

Heritability is a function of the breeding population and the conditions under which the study is conducted (Falconer, 1981). When our results are compared with those reported by previous researchers, some traits had similar heritability. The heritability estimate (regression coefficient rather than correlation coefficient) for % kernel was 0.67 in Thompson's data set (1977), and 0.72 in Romisondo' data set (1983). Both are slightly lower than the 0.87 reported here. The populations studied by Thompson and Romisondo had a narrow genetic base, while the population in this paper had a wide genetic base. The more genetic diversity in the population, the higher the heritability likely will be (Falconer, 1981). The heritability estimate for fiber amount in Thompson's data set (1977) was 0.55, nearly identical to the 0.56 reported in this paper. The low heritabilities in Thompson's data set (1977) for number of nuts per cluster and husk length, 0.10 and 0.30 respectively, were based on ratings, which are less precise than actual measurement. We used actual counts for nuts and clusters, and made measurements of husk length and obtained higher heritability estimates for both traits, 0.67 and 0.82, respectively. Mehlenbacher and Smith (1988) found blanching ability to have moderately high heritability (0.48), while our result for this trait was 0.64. Mehlenbacher and Smith (1988) evaluated blanching ability after roasting the kernels at 130°C for 13.5 minutes, while our

kernels were roasted at 122.5°C for 20 minutes. This difference in treatments might have caused different estimates in these two data sets.

When our results are compared with the same or similar traits in nut and tree fruit crops, similar heritabilities were observed for some traits (Table 2.4). High heritability estimates were observed for phenological traits (Table 2.4). Many factors affected these results because the studied populations, conditions and types of measurements were different. However, the high heritability estimates found for nearly all traits in the tree fruit and nut crops indicates that additive gene action predominates. Therefore, the selection of parents based on their phenotypic values is recommended, and genetic advance is expected to be rapid. When heritability estimates are low to moderate, selection of parents based on phenotypes may still be effective and genetic advance satisfactory (Hansche et al., 1972b; Thompson and Baker, 1993). When heritability estimates are very low, the development of more precise objective measures and growing under more uniform conditions can reduce measurement error and thus increase heritability estimates (Hansche et al., 1966, 1972b). Our results on husk length and number of nuts per cluster illustrate this point. If traits have very low heritability, and precise measurements do not improve the heritability, it may indicate a lack of additive genetic variation for the trait and a need to introduce new germplasm.

Table 2.4 Heritability estimates for some traits in tree fruit and nut crops

Species	Trait	Heritability	Sample size	Data transformation	Reference
Almond (*Prunus amygdalus* Batsch.)	Nut weight	0.81±0.17	25 nuts	Original data	Kester et et al., 1977
	Kernel length	0.77±0.17	10 nuts		
	Kernel thickness	0.71±0.21	10 nuts		
	Kernel weight	0.64±0.17	25 nuts		
	Kernel width	0.62±0.17	10 nuts		
	First flowering time	0.93±0.06		Uncorrected day unit	Dicenta et al., 1993a
	Full flowering time	0.99±0.07			
	Final flowering time	0.84±0.06			
	Duration of flowering	1.05±0.10			
	Time of maturity	0.83±0.08			
	Duration of maturity	0.76±0.08			
	Nut weight	1.00±0.10	50 nuts	Seasonally corrected data	Dicenta et al., 1993b
	Kernel weight	0.71±0.13	50 nuts		
	Percent kernel	0.56±0.12	50 nuts		
Pecan (*Carya illinoinensis* (Wangenh) K. Koch)	Nut weight	0.35		Seasonally corrected	Thompson and Baker , 1993
	Kernel weight	0.38			
	Percent karnel	0.32			
Walnut (*Juglas regia* L.)	Leafing date	0.96±0.02		Seasonally corrected day unit	Hansche et al., 1972b
	Harvest date	0.85±0.02			
	Nut length	0.82±0.03	10 nuts		
	Nut suture	0.89±0.04	10 nuts		
	Nut cheek	0.97±0.04	10 nuts		
	Nut weight	0.86±0.04	10 nuts		
	Kernel weight	0.87±0.04	10 nuts		
Apple (*Malus domestica* Borkh.)	Ripening	0.92±0.07		Days relative to standard variety	Tancred et al., 1995
Sweet cherry (*Prunus avium*. L)	1st bloom date	0.65±0.04		Seasonally corrected day unit	Hansche et al., 1966
	Full bloom date	1.00±0.06			
	Ripe date	0.88±0.03			
Peach (*Prunus persica* L.)	Date of full bloom	0.78		Uncorrected interval	De Souza et al., 1998a
	Date of ripening	0.94			
	Fruit develop-ment	0.91			
	Full bloom date	0.39		Seasonally corrected day unit	Hansche et al., 1972b
	Ripe date	0.84			
	Short fruit devlopment period	0.74±0.10		Seasonally corrected interval	Vilella-Morales et al., 1981
	Date of bloom	0.98±0.30			

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CHAPTER 3

ESTIMATES OF VARIANCE COMPONENTS AND BROAD SENSE HERITABILITIES OF 17 TRAITS IN HAZELNUT

Abstract

Data for three years from 41 genotypes (23 cultivars and 18 selections) represented by 77 trees were used to analyze variance components and heritability in the broad sense of 17 traits in hazelnut (*Corylus avellana* L.). Genotypic variance accounted for most of the phenotypic variance. Although significant, the genotype X year interaction only accounted for a very small part of the phenotypic variance. Heritabilities ranged from 0.79 for nut maturity to 0.99 for nut length. Compared with heritability in the narrow sense, broad sense heritability was significantly higher for most studied traits. It suggests that important non-additive genetic variance exists in the OSU hazelnut breeding population. In addition, the allocation of resources in the evaluation of these traits will be discussed.

Introduction

Estimation of variance components in a breeding program can provide extremely useful information to breeders. It can be used to calculate heritability so that breeders can select parents and plan crosses more efficiently for improvement of target traits (Tancred et al., 1995). Such studies can also provide information in determining the most efficient design for genotype evaluation, and the most effective manner of replicating measurements to adequately discriminate genetically superior from inferior offspring (Hansche et al., 1972).

In general, breeders of various species can use different experimental designs and materials to analyze variance components and estimate various genetic parameters of interest. When variance components are computed with data from varieties and/or selections (lines), heritability in the broad-sense can be calculated (Martin, 1990; Singh et al., 1993; Singh and Ceccarelli, 1995). When heritability is calculated as the ratio of variance components, there are several methods to estimate precision of the estimates (Dieters et al., 1995b; Knapp, 1985), including standard errors and exact confidence intervals. If the distribution of heritability is not known, the ratio of mean squares, is known to have an F-distribution, and an exact confidence interval for the heritability estimate can be derived (Knapp, 1986; Knapp and Bridges, 1987; Knapp et al., 1985).

In tree fruit and nut crop breeding, data for the analysis of variance components comes from observations in breeding programs at a fixed place over a period of several years (Kester et al., 1977; Mehlenbacher et al., 1993). Data analysis allows estimation of variance components for genotypes, years, and genotype X year interaction. The relative importance of these components aids breeders in deciding on the number of years to evaluate entries for target traits to distinguish superior from inferior genotypes.

Hazelnut is a very important nut crop, whose importance ranks second or third after almond and walnut (Mehlenbacher, 1994). The OSU hazelnut breeding program has very clearly defined objectives for developing improved varieties for the kernel market (Mehlenbacher, 1994). For most target traits, there is little information about genetic parameters although several reports estimated narrow-sense heritabilities by regression of offspring means on mid-parent values (Mehlenbacher, 1994; Thompson, 1977).

Mehlenbacher et al. (1993) estimated variance components of traits related to defective kernels and nuts.

The objectives of this paper are: 1) to estimate variance components of 17 traits in hazelnut for data collected over a 3-year period; 2) to calculate broad-sense heritabilities of these traits, including exact confidence intervals for these estimates; 3) to use these results to explore implications for cultivar improvement in hazelnut.

Materials and Methods

Plant materials

Seventy seven trees representing 41 genotypes were used to estimate variance components for 17 traits. Thirty-six of the genotypes were represented by two trees. Detailed information was presented in Chapter 2. For all traits except nut maturity, the observation period lasted three years. The first year began in August 1994 and ended in March 1995. The second year began in August 1995 and ended in April 1996. The third year (1996-1997) had the same observation period as the second year. Nut maturity was only observed in the second and third years. Most trees were located at the Smith vegetable research farm of Oregon State University in Corvallis, Oregon. A few trees were located at the nearby National Clonal Germplasm Repository of USDA.

Observation standards

They were described in Chapter 2. Here we present the sample size for each trait. Nut length (NL), width (NW) and depth (ND) had 20-nut samples selected at random for every tree. Nut shape index (SI), and compression index (CI) had the same sample size

as nut length, width and depth. For nut weight (NWT), kernel weight (KWT), % kernel (%K), fiber amount (FA) and blanching ability (BA), two samples were evaluated for each tree. Time of leafing out (LO), time of catkin elogation (TCE), date of opening of female flowers (DOFF) and nut maturity (NM) were recorded for each tree. Number of nuts per cluster (NNPC) of each tree was based on counts from three limbs in different parts of the tree. Husk length (HL) was measured on 10 husks from every tree. Relative husk length (RHL) was calculated as the ratio of husk length to nut length, using the previously calculated averages for these two traits for each tree.

Statistical methods

Two statistical models were used to estimate variance components, one for traits evaluated from more than one sample per tree, and a second model for traits in which a single observation was recorded on each tree in each year.

Model I was $Y_{ijkl} = \mu + G_i + T_j(G_i) + Y_k + (GY)_{ik} + [YT(G)]_{ijk} + \varepsilon_{ijkl}$, where Y_{ijkl} was a value from the lth sample from the jth tree of the ith genotype in the kth year, μ was the overall population mean, G_i the effect of genotype, $T_j(G_i)$ the effect of tree within genotype, Y_k the year effect, $(GY)_{ik}$ the genotype by year interaction, $[YT(G)]_{ijk}$ the interaction of year with tree nested within genotype, and ε_{ijkl} sampling error. This model was used to estimate variance components for all kernel and nut traits except RHL. The model was originally used to describe variance components related to nut and kernel defects in hazelnut (Mehlenbacher et al., 1993).

Model II was $Y_{ijk} = \mu + G_i + T_j(G_i) + Y_k + (GY)_{ik} + \varepsilon_{ijk,}$ where Y_{ijk} was a value from the jth tree of the ith genotype in the kth year, μ was the overall population mean, G_i the effect of genotype, $T_j(G_i)$ the effect of tree within genotype, Y_k the year effect, $(GY)_{ik}$ the genotype by year interaction, and ε_{ijk} error term. The model was used to estimate variance components for phenological traits and RHL. These are traits for which a single observation was taken on each tree in each year.

All effects in these models listed above were assumed to be random so that these experimental results could be extended to other populations and years. The VARCOMP procedure of SAS version 6.12 for Windows (SAS Institute, 1994) was used to estimate variance components. The significance levels of the components and mean squares (m.s.) were determined using the GLM procedure. The LSMEANS option of the GLM procedure was used to calculate least square means for genotypes in each year to observe rank changes of genotypes from year to year.

Based on these models, we then set up ANOVA tables including expected mean squares [E(m.s.)] as described by Searle (1971) and Wricke and Weber (1986) (Tables 3.1, 3.2). The equations for expected mean squares can be solved to obtain estimates of variance components.

The formulas for heritabilities of all studied traits are listed below.

The formula for heritability of kernel and nut traits:

Table 3.1 ANOVA Table for Model I (Balanced Data)

Source	df	m.s.	E(m.s.)
Y	not relevant		
G	$d.f._1 = i - 1$	m_1	$\theta_1 = \sigma_e^2 + l\sigma_{t(g)y}^2 + lj\sigma_{gy}^2 + kl\sigma_{t(g)}^2 + jkl\sigma_g^2$
T(G)	$d.f._2 = i(j - 1)$	m_2	$\theta_2 = \sigma_e^2 + l\sigma_{t(g)y}^2 + lk\sigma_{t(g)}^2$
GY	$d.f._3 = (i - 1)(k - 1)$	m_3	$\theta_3 = \sigma_e^2 + l\sigma_{t(g)y}^2 + jl\sigma_{gy}^2$
T(G)Y	$d.f._4 = i(j - 1)(k - 1)$	m_4	$\theta_4 = \sigma_e^2 + l\sigma_{t(g)y}^2$
E	$d.f._5 = ijk(l - 1)$	m_5	$\theta_5 = \sigma_e^2$

Variance components: $\sigma_g^2 = \dfrac{m_1 - m_2 - m_3 + m_4}{jkl}$; $\sigma_{t(g)}^2 = \dfrac{m_2 - m_4}{lk}$; $\sigma_{gy}^2 = \dfrac{m_3 - m_4}{jl}$;

$\sigma_{t(g)y}^2 = \dfrac{m_4 - m_5}{l}$; $\sigma_e^2 = m_5$.

Table 3.2 ANOVA Table for Model II (Balanced Data)

Source	df	m.s.	E(m.s.)
Y	not relevant		
G	$d.f._1 = i - 1$	m_1	$\theta_1 = \sigma_e^2 + j\sigma_{gy}^2 + k\sigma_{t(g)}^2 + jk\sigma_g^2$
T(G)	$d.f._2 = i(j - 1)$	m_2	$\theta_2 = \sigma_e^2 + k\sigma_{t(g)}^2$
GY	$d.f._3 = (i - 1)(k - 1)$	m_3	$\theta_3 = \sigma_e^2 + j\sigma_{gy}^2$
E	$d.f._4 = i(k - 1)(j - 1)$	m_4	$\theta_4 = \sigma_e^2$

Variance components: $\sigma_g^2 = \dfrac{m_1 - m_2 - m_3 + m_4}{jk}$; $\sigma_{t(g)}^2 = \dfrac{m_1 - m_4}{k}$; $\sigma_{gy}^2 = \dfrac{m_3 - m_4}{j}$;

$\sigma_e^2 = m_4$.

$$h^2 = \frac{\frac{m_1 - m_2 - m_3 + m_4}{jkl}}{\frac{m_1}{jkl}} = 1 - \frac{m_2 + m_3 - m_4}{m_1} =$$

$$\frac{\sigma_g^2}{\frac{\sigma_e^2}{jkl} + \frac{\sigma_{l(g)y}^2}{jk} + \frac{\sigma_{gy}^2}{k} + \frac{\sigma_{l(g)}^2}{j} + \sigma_g^2}$$

The formula for heritability of phenological traits and RHL:

$$h^2 = \frac{\frac{m_1 - m_2 - m_3 + m_4}{jk}}{\frac{m_1}{jk}} = 1 - \frac{m_2 + m_3 - m_4}{m_1} = \frac{\sigma_g^2}{\frac{\sigma_e^2}{jk} + \frac{\sigma_{gy}^2}{k} + \frac{\sigma_{l(y)}^2}{j} + \sigma_g^2}$$

These ANOVA tables (Tables 3.1, 3.2) were constructed for a balanced subset, i.e. only genotypes which had two trees and the same number of samples each year, were included for data analysis. However, our whole data set was slightly unbalanced. The procedure for setting up ANOVA tables, and expected mean squares was the same; the correct coefficients were generated by the GLM procedure.

Heritability will be assumed to have an F-distribution. Its precision will be represented with exact confidence intervals. The calculation methods were as described by Knapp (1986), Knapp and Bridges (1987) and Knapp et al. (1985). When heritability was estimated with the pooled data set, exact confidence intervals were calculated by the formula listed below:

$P\{1 - [(M'/M'')F_{\alpha/2:df'',df'}]^{-1} \leq 1 - E(M')/E(M'') \leq 1 - [(M'/M'')F_{1-\alpha/2:df'',df'}]^{-1}\} = 1 - \alpha$,

where M'' was m_1, M' equaled $m_2 + m_3 - m_4$, df'' was degrees of freedom associated with M'', and df' was degrees of freedom associated with M'. We calculated 95% exact confidence intervals for all traits.

Results

Type I and REML methods of the VARCOMP procedure were used to estimate variance components for pooled unbalanced and balanced data sets, and all methods led to the same conclusions, i.e., the genotype variance obviously ranked first in magnitude for all traits except CI (Table 3.3). The relative magnitude of the variances for tree, year, genotype by year interaction, interaction of year with tree nested within genotype, and error depended on the traits. Because REML is considered the best procedure to estimate variance components for unbalanced data (Dieters, et al., 1995a; Swallow and Monahan, 1984), only results estimated by REML are shown.

To evaluate the relative importance of various variance components in contributing to phenotypic variance, genotypic variance was set equal to 1, and the magnitude of other variance components was expressed relative to genotypic variance (Table 3.4). Genotypic variance was very high for all traits. Sampling variance was not important for traits related to nuts and kernels. The error term for phenological traits was larger than the component for tree nested in genotype because the error term actually included the interaction of year with tree nested in genotype. Genotype by year interaction was more important than tree nested in genotype for all traits. Genotype by

Table 3.3 Variance components of 17 traits in hazelnut for unbalanced data with REML method

Trait	G	T(G)	Y	G x Y	T(G) x Y	Error
NL	7.277	0.092	0.062	0.100	0.068	1.121
NW	4.019	0.028	0.542	0.306	0.139	0.830
ND	4.941	0.050	0.267	0.194	0.117	0.662
SI	.01050	.00014	.00048	.00056	.00015	.00290
CI	.00272	.00006	.00011	.00017	.00009	.00283
NWT	46.226	1.502	2.745	7.480	2.652	1.817
KWT	7.951	0.180	0.955	1.411	0.536	0.377
%K	.00202	.00003	.00005	.00008	.00008	.00007
FA	0.445	0.000	0.043	0.095	0.131	0.011
BA	2.380	0.033	0.094	0.197	0.135	0.157
NNPC	0.263	0.018	0.024	0.069	0.015	0.053
HL	41.788	1.303	0.149	0.741	0.213	9.952
RHL	.07876	.00096	.00135	.00059		.00834
NM	2.486	0	0.381	0.718		0.694
DOFF	6.044	0.109	2.955	2.415		0.604
TCE	4.192	0.063	0.680	0.875		0.269
LO	1.515	0.032	0.372	0.105		0.135

Table 3.4 Relative variance components and phenotypic variance of 17 traits

Trait	G	T(G)	G x Y	T(G) x Y	Error	Phenotypic
NL	1.0000	0.0068	0.0046	0.0017	0.0014	1.0145
NW	1.0000	0.0037	0.0254	0.0062	0.0019	1.0372
ND	1.0000	0.0054	0.0131	0.0042	0.0012	1.0239
SI	1.0000	0.0071	0.0178	0.0026	0.0025	1.0300
CI	1.0000	0.0118	0.0209	0.0059	0.0093	1.0560
NWT	1.0000	0.0173	0.0540	0.0104	0.0037	1.0854
KWT	1.0000	0.0121	0.0595	0.0122	0.0045	1.0883
%K	1.0000	0.0079	0.0132	0.0071	0.0032	1.0314
FA	1.0000	0.0000	0.0709	0.0529	0.0234	1.1472
BA	1.0000	0.0074	0.0276	0.0102	0.0061	1.0513
NNPC	1.0000	0.0376	0.0872	0.0103	0.0131	1.1482
HL	1.0000	0.0169	0.0059	0.0009	0.0044	1.0281
RHL	1.0000	0.0066	0.0025		0.0196	1.0287
NM	1.0000	0.0000	0.1440		0.0762	1.2203
DOFF	1.0000	0.0096	0.1331		0.0181	1.1607
TCE	1.0000	0.0080	0.0696		0.0116	1.0892
LO	1.0000	0.0113	0.0230		0.0162	1.0505

year interaction was a relatively small part of phenotypic variance, accounting for less than 5% of the genotypic variance for most traits, and slightly higher for TCE, FA, NNPC. The relative component for genotype by year interaction was highest for DOFF (0.13) and NM (0.14). All traits had high heritability estimates but FA, NNPC, DOFF and NM had wider exact confidence intervals (Table 3.5).

When means were calculated for each genotype in each year, slight changes in genotype rank from year to year were observed. For traits like %K with heritability 0.962 and nut length with heritability 0.986, the genotype rank changed only slightly, and values were quite consistent from year to year (Tables 3.6 and 3.7). Similar results were observed for NW, ND, SI, CI, and BA. For traits with larger relative genotype by year interaction and lower heritability, changes in genotype rank were more striking, as for NNPC (Table 3.8), and NM (Table 3.9).

Discussion

Advanced experimental designs require replication, randomization and blocking of treatments to reduce experimental error (Petersen, 1994). But these conditions are often not met in the plantings established as part of breeding programs in perennial tree fruit and nut crops. Such plantings often have no specific experimental design (Hansche et al., 1972; Kester et al., 1977; Thompson and Baker, 1993).

However, plantings of cultivars and advanced selections usually include more than one tree of each genotype, and data are collected over a period of several years. These plantings can be viewed as nested designs (trees nested within genotypes) with repeated measurements. In many ways they resemble a split-plot design, with genotypes

Table 3.5 Estimates of heritability with pooled data from three years

Traits	df'	df''	M'	M''	H	Lower H	Upper H
NL	58	40	11.572	847.9	0.986	0.976	0.992
NW	72	40	15.867	427.7	0.966	0.937	0.979
ND	71	40	12.81	512.1	0.977	0.957	0.986
SI	79	40	0.033	1.228	0.972	0.955	0.985
CI	54	40	0.014	0.301	0.948	0.917	0.974
NWT	83	40	40.666	545.9	0.921	0.875	0.958
KWT	79	40	7.24	90.83	0.919	0.866	0.955
%K	57	40	0.0007	0.023	0.962	0.944	0.982
FA	45	40	0.585	5.069	0.888	0.789	0.938
BA	59	40	1.298	27.53	0.951	0.918	0.974
NNPC	81	40	0.549	4.114	0.871	0.776	0.924
HL	39	40	83.977	2152	0.973	0.926	0.979
RHL	30	40	0.013	0.352	0.972	0.926	0.981
NM	28	40	1.966	11.661	0.820	0.651	0.914
DOFF	70	40	5.155	37.570	0.862	0.766	0.923
TCE	84	40	1.959	23.49	0.918	0.861	0.953
LO	58	40	0.418	8.829	0.952	0.917	0.974

[z] df' is degrees of freedom associated with M', df'' is degrees of freedom associated with M'', M' is ($m_2 + m_3 - m_4$) in heritability formula, M'' is m_1, H is heritability in the broad sense, lower H is lower 95% exact confidence interval of broad sense heritability and upper H is upper 95% exact confidence interval of broad sense heritability.

Table 3.6 Genotype means in different years for %K

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Gem	0.380	Aurea	0.375	026.072	0.390
026.072	0.388	Gem	0.380	Aurea	0.395
Aurea	0.400	026.072	0.383	Hall's Giant	0.400
Hall's Giant	0.403	Hall's Giant	0.383	Gem	0.423
Brixnut	0.428	Brixnut	0.420	Brixnut	0.433
Sant Jaume	0.430	Segorbe	0.438	Sant Jaume	0.438
Segorbe	0.438	244.001	0.440	GH88-14	0.440
TGDL	0.445	245.094	0.440	Segorbe	0.450
T. di Giffoni	0.450	183.060	0.443	245.094	0.458
GH88-14	0.455	GH88-14	0.445	VR17-15	0.458
GH140-4	0.458	Sant Jaume	0.448	244.001	0.463
Tonda Romana	0.458	Fusco Rubra	0.455	TGDL	0.465
245.094	0.460	VR17-15	0.460	Contorta	0.470
244.001	0.463	023.017	0.468	Fusco Rubra	0.473
Fusco Rubra	0.463	GH140-4	0.470	GH140-4	0.475
179.043	0.465	039.044	0.473	T. di Giffoni	0.478
VR17-15	0.465	Contorta	0.475	054.039	0.480
183.060	0.473	T. di Giffoni	0.475	183.060	0.483
054.039	0.475	Willamette	0.478	179.043	0.485
186.080	0.483	054.039	0.480	233.007	0.485
023.017	0.488	179.043	0.480	Willamette	0.490
Contorta	0.490	Ribet	0.480	023.017	0.498
Willamette	0.495	233.007	0.490	162.017	0.500
039.044	0.500	TGDL	0.490	Negret	0.500
233.007	0.500	225.077	0.493	Ribet	0.503
246.128	0.500	Negret	0.493	246.128	0.505
Negret	0.503	186.080	0.495	186.080	0.508
Ribet	0.503	Tonda Romana	0.495	VR20-11	0.510
055.077	0.505	162.017	0.498	Tonda Romana	0.513
162.017	0.508	Mortarella	0.498	055.077	0.515
VR20-11	0.510	VR20-11	0.503	225.077	0.525
225.077	0.528	055.077	0.505	Daviana	0.530
Daviana	0.530	246.128	0.510	039.044	0.533
055.129	0.535	Daviana	0.513	Mortarella	0.540
RG1	0.535	Casina	0.523	Birk5-6	0.543
Birk5-6	0.538	Birk5-6	0.533	Casina	0.545
054.021	0.540	255.003	0.538	054.021	0.560
Mortarella	0.540	RG1	0.550	RG1	0.560
Casina	0.545	055.129	0.553	255.003	0.563
255.003	0.548	054.021	0.555	055.129	0.568
166.034	0.560	166.034	0.555	166.034	0.573

Table 3.7 Genotype means in different years for nut length

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Fusco Rubra	15.03	Fusco Rubra	14.66	Fusco Rubra	15.86
246.128	15.51	026.072	15.80	246.128	16.03
026.072	15.92	246.128	16.03	026.072	16.09
GH140-4	17.12	GH140-4	16.65	Aurea	17.23
166.034	17.30	166.034	16.96	GH140-4	17.59
Aurea	17.53	186.080	17.18	166.034	17.71
Casina	17.67	Aurea	17.36	183.060	17.87
183.060	18.08	Casina	17.37	186.080	18.48
186.080	18.17	183.060	17.46	054.039	18.66
VR17-15	18.43	VR17-15	17.59	Casina	18.71
162.017	18.71	RG1	17.96	TGDL	18.86
054.039	18.73	225.077	18.32	055.129	18.94
VR20-11	18.86	054.039	18.39	RG1	18.95
RG1	19.00	162.017	18.40	VR20-11	19.10
Sant Jaume	19.04	VR20-11	18.57	055.077	19.19
Birk5-6	19.16	TGDL	18.91	162.017	19.19
055.129	19.18	255.003	19.01	VR17-15	19.29
225.077	19.38	Sant Jaume	19.08	Sant Jaume	19.43
TGDL	19.42	055.077	19.09	225.077	19.76
055.077	19.43	245.094	19.11	054.021	19.76
255.003	19.48	Birk5-6	19.23	179.043	19.90
179.043	19.69	055.129	19.42	T. di Giffoni	20.04
245.094	19.73	T. di Giffoni	19.47	Ribet	20.11
244.001	20.32	054.021	19.64	245.094	20.22
Negret	20.33	179.043	19.65	255.003	20.25
Mortarella	20.34	Negret	19.69	233.007	20.33
054.021	20.40	233.007	19.74	Birk5-6	20.34
T. di Giffoni	20.55	Tond Romana	19.77	Mortarella	20.36
023.017	20.56	Willamette	19.83	Tond Romana	20.46
Ribet	20.71	023.017	19.93	Segorbe	20.50
233.007	20.72	Ribet	20.05	244.001	20.66
Tond Romana	20.72	Mortarella	20.38	Willamette	20.67
Segorbe	20.94	244.001	20.41	Negret	20.80
Willamette	21.15	Segorbe	20.57	023.017	20.95
Contorta	21.41	Contorta	20.64	Contorta	21.02
039.044	23.24	039.044	23.21	039.044	22.80
GH88-14	23.34	GH88-14	23.22	Hall's Giant	23.26
Hall's Giant	23.96	Hall's Giant	23.37	GH88-14	23.52
Brixnut	24.44	Brixnut	25.37	Brixnut	24.50
Daviana	25.50	Daviana	26.29	Daviana	26.31
Gem	30.71	Gem	29.52	Gem	28.92

Table 3.8 Genotype means in different years for number of nuts per cluster

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Aurea	1.29	Aurea	1.06	Aurea	1.14
026.072	1.44	Contorta	1.12	246.128	1.22
VR20-11	1.50	Daviana	1.36	GH88-14	1.23
246.128	1.70	VR20-11	1.40	026.072	1.33
Birk5-6	1.71	039.044	1.44	Contorta	1.33
Contorta	1.71	246.128	1.52	VR20-11	1.44
Daviana	1.82	166.034	1.57	Hall's Giant	1.46
054.039	1.86	Hall's Giant	1.66	Negret	1.49
166.034	1.91	026.072	1.69	Birk5-6	1.53
039.044	1.91	Negret	1.74	Daviana	1.61
055.077	2.01	GH88-14	1.84	166.034	1.62
Ribet	2.09	Willamette	1.87	183.060	1.77
T. d. Giffoni	2.09	255.003	1.87	Casina	1.77
GH88-14	2.16	Birk5-6	1.94	039.044	1.80
TGDL	2.18	183.060	2.00	Fusco Rubra	1.92
Segorbe	2.21	179.043	2.02	Willamette	1.92
Fusco Rubra	2.23	Sant Jaume	2.12	Segorbe	1.97
Casina	2.24	TGDL	2.20	244.001	1.97
Hall's Giant	2.27	T. d. Giffoni	2.21	Sant Jaume	1.98
183.060	2.32	055.129	2.27	GH140-4	2.00
255.003	2.35	Ribet	2.29	055.077	2.04
Negret	2.38	Gem	2.31	179.043	2.06
GH140-4	2.40	Casina	2.32	233.007	2.06
162.017	2.42	RG1	2.33	RG1	2.09
RG1	2.43	055.077	2.34	Ribet	2.16
055.129	2.46	186.080	2.45	T. d. Giffoni	2.17
Gem	2.50	GH140-4	2.54	TGDL	2.19
179.043	2.68	Fusco Rubra	2.55	Gem	2.25
186.080	2.70	Segorbe	2.60	055.129	2.33
Sant Jaume	2.70	244.001	2.67	255.003	2.37
Tonda Romana	2.71	162.017	2.76	054.039	2.45
233.007	2.72	VR17-15	2.80	Tonda Romana	2.66
Willamette	2.88	Mortarella	2.83	VR17-15	2.66
VR17-15	2.96	Tonda Romana	2.90	186.080	2.67
054.021	3.00	Brixnut	2.96	245.094	2.73
244.001	3.09	245.094	2.97	Brixnut	2.80
Brixnut	3.12	023.017	3.09	054.021	2.84
245.094	3.12	225.077	3.18	162.017	2.90
225.077	3.28	054.039	3.31	023.017	3.09
023.017	3.53	233.007	3.63	Mortarella	3.10
Mortarella	4.41	054.021	3.69	225.077	3.12

Table 3.9 Genotype means in different years for nut maturity

1995		1994	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
055.129	1	026.072	1
TGDL	1	055.129	1
Sant Jaume	1.5	Fusco Rubra	1
026.072	2	Sant Jaume	1
Fusco Rubra	2	TGDL	1
055.077	3	246.128	2.5
179.043	3	255.003	3
225.077	3	Segorbe	3
255.003	3	T. d. Giffoni	3.5
Mortarella	3	054.021	4
166.034	4	054.039	4
186.080	4	055.077	4
Daviana	4	186.080	4
GH140-4	4	225.077	4
039.044	4.5	Daviana	4
246.128	4.5	GH140-4	4
054.039	5	Hall's Giant	4
Hall's Giant	5	Mortarella	4
RG1	5	039.044	4.5
VR17-15	5	179.043	4.5
023.017	6	Birk5-6	4.5
233.007	6	Negret	4.5
Aurea	6	023.017	5
Contorta	6	162.017	5
GH88.14	6	166.034	5
Ribet	6	183.060	5
Segorbe	6	244.001	5
Willamette	6	Casina	5
244.001	6.5	GH88.14	5
Birk5-6	6.5	Tonda Romana	5
Negret	6.5	VR17-15	5
T. d. Giffoni	6.5	VR20-11	5
054.021	7	Willamette	5
183.060	7	RG1	5.5
Casina	7	233.007	6
Gem	7	245.094	6
Tonda Romana	7	Aurea	6
VR20-11	7	Brixnut	6
Brixnut	7.5	Contorta	6
162.017	10	Ribet	6.5
245.094	10.5	Gem	7

as the main plots and years and genotype by year interaction as sub-plots. If there are sub-samples from the same tree for measurements of a trait, the interaction of years with trees nested within genotypes can be used as the sub-plot error term. These two models are presented as Model I and Model II in this paper. If the interaction term in the sub-plot is statistically significant, comparison of genotype means within each subplot is needed. Because Model I and Model II had significant genotype x year interaction, we compared genotype means in each year separately.

When heritability in the broad sense is estimated, breeders are interested in variance components in such designs. Mehlenbacher et al. (1993) first described Model I and applied it to the analysis of variance of defective nut and kernel traits. We estimated heritability in the broad sense with variance components. Broad sense heritability is the ratio of genetic variance to phenotypic variance, which includes additive genetic variance and non-additive genetic variance (Falconer, 1981). Compared with narrow sense heritability (Chapter 2), broad sense heritability was significantly higher, which may suggest that important non-additive genetic variance exists in the OSU hazelnut breeding population for most studied traits. In addition, the magnitude of broad sense heritability indicates the stability of a trait. The larger the heritability, the more consistent the trait from year to year, sample to sample, and tree to tree.

Broad sense heritability estimates can also be used to effectively allocate resources for evaluation. Hansche et al. (1965) estimated broad sense heritability for 18 quantitative characters observed in a *Prunus avium* variety collection, computed on the basis of a single observation and on observations in each of 2 years. He concluded that observation over a period of 2 or 3 years would be an effective means to distinguish

superior from inferior genotypes. However, it is comparatively expensive because each replication retards the progress of selection by one year. Spatial replication, in so far as it circumvents this delay, is probably less expensive.

In the evaluation of hazelnut seedlings for these traits, it is obvious that one season's evaluation is enough for nut length, nut width, nut depth, nut shape index, nut compression index, % kernel, blanching ability, husk length, relative husk length and time of leafing out if samples are sufficiently large. We used 20-nut samples for evaluation of nut length, nut width, nut depth, nut shape index and nut compression index in our original data set. In practice, visual examination of just a few nuts would be sufficient to judge if they were round. Although nut number per cluster had high heritability, its confidence interval was relatively wide, and our samples usually came from 3 branches, each of which had at least 15 clusters. The trait is not suitable for evaluation of very young trees because they have too few nuts. Fiber amount is not an important trait if the final product is a blanched kernel without a pellicle. But if kernels are sold raw with pellicles attached, it is obvious that the trait is important. At least 2 years' evaluation is recommended because ratings vary from one year to the next. The situation is similar for TCE. For nut maturity and DOFF, more than a single year's observation is needed to distinguish the best from poor genotypes because there was a large genotype x year interaction for these two traits.

Greene et al. (1992) noticed that some traits in American sycamore (*Platanus occidentalis* L.), such as height and volume, increased in their heritability as the trees aged. Mehlenbacher et al. (1993) observed that older seedlings and larger trees in replicated yield trials would be more likely to provide information on which genotypes

were prone to poorly filled nuts. We did not observe obvious regular change of these traits from year to year in our observation period.

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CHAPTER 4

ESTIMATION OF CORRELATION COEFFICIENTS AMONG 17 TRAITS AND THEIR IMPLICATIONS IN THE OSU HAZELNUT BREEDING PROGRAM

Abstract

Thirty five hazelnut (*Corylus avellana* L.) progenies and 41 parent genotypes were used to estimate phenotypic and genetic correlation coefficients among 17 nut, kernel and phenological traits from August, 1994 to March, 1996. Correlation coefficients were large and positive for nut size traits (nut length, width, depth, nut weight and kernel weight). Phenological traits (date of opening of female flowers, time of catkin elongation and time of leafing out) were also highly and positively correlated. But most other traits were uncorrelated with each other. These results and their implications in the OSU hazelnut breeding program are discussed.

Introduction

A variety of a tree fruit or nut crop is a homogeneous population of heterozygous plants. The traditional approach to genetic improvement is to cross highly heterozygous parent clones, select the best of the resulting seedlings, and release it as a new variety if warranted. Multiple traits must be considered in evaluating seedlings and selections.

In the Oregon State University hazelnut breeding program, the traits to be improved include: round nuts of medium size, high % kernel (%K), precocity and high yield, easily blanched kernels, few nut and kernel defects, early maturity and free-falling nuts (Mehlenbacher, 1994). The standards for these traits were listed by Mehlenbacher

(1995) . It is obvious that directional selection is used to improve %K, blanching ability, and nut maturity, while stabilizing selection is used to improve nut shape and size, as intermediate values are desired for these traits.

Because many traits are to be improved simultaneously, it is important to know how the traits are interrelated. Is indirect selection better than direct selection for some traits? Might performance of phenological traits predict that of nut and kernel traits? To answer these questions, estimation of correlation coefficients in a breeding program as well as heritability in the narrow sense will be helpful. Breeders working with fruit and nut crops have estimated correlation coefficients, most often phenotypic correlation coefficients, of traits in species, including grape (Firoozabady and Olmo, 1987), hazelnut (Mehlenbacher et al., 1993), pecan (Thompson and Baker, 1993), peach (De Souza et al., 1998a, 1998b), sweet cherry (Hansche et al., 1966) and walnut (Hansche et al., 1972).

Estimation of correlation coefficients may provide some additional important information for breeders (Falconer and Mackay, 1996). They allow: 1) comparison of indirect with direct selection; 2) computation of correlated response in a second trait if selection pressure is applied to the first; and 3) establishment of selection strategy.

In this paper, we present coefficients of simple, phenotypic, and genetic correlation for 13 nut and kernel traits and 4 phenological traits in hazelnut and discuss the implications of these estimates in the breeding program.

Materials and Methods

Plant materials and observation standards

Seventy seven trees representing 41 genotypes (1-2 trees of each of 23 cultivars and 18 selections) were used to estimate parent values. The seedlings resulted from 35 controlled crosses involving these 41 parents made in 1988 and 1989. For most traits, the observation period lasted two years. Data from Aug. 1994 to April, 1995 is presented as 1994 data, and data from Aug. 1995 to April, 1996 is presented as 1995 data.

The observed traits include nut length (NL), nut width (NW), nut depth (ND), nut shape index (NSI), nut compression index (NCI), nut weight (NWT), kernel weight (KWT), % kernel (%K), fiber amount (FA), blanching ability (BA), husk length (HL), relative husk length (RHL), number of nuts per cluster (NNPC), nut maturity (NM), date of opening of female flowers (DOFF), time of catkin elogation (TCE), and time of leafing out (LO). These traits and how they were measured were described in detail in Chapter 2.

Simple and phenotypic correlations

Simple and phenotypic correlations were calculated as Pearson product-moment correlation coefficients (Firoozabady and Olmo, 1987; Hansche et al., 1972). The formula for a correlation coefficient is $r = \frac{\sum_{i=1}^{n}(X-\overline{X})(Y-\overline{Y})}{\sqrt{\sum_{i=1}^{n}(X-\overline{X})^2\sum_{i=1}^{n}(Y-\overline{Y})^2}}$, where X is a phenotypic value of one trait, and Y is a phenotypic value of the other trait, and $\overline{X}$ and $\overline{Y}$ are average phenotypic values for these two traits respectively. For simple correlation

coefficient calculation, x and y represent phenotypic values for 2 traits on a single tree. For phenotypic correlation coefficient calculation, x and y represent progeny mean phenotypic values for 2 traits. When x or y had a missing value, the individual or cross was not included in the calculation. We also used this formula to calculate simple and phenotypic correlations for the same trait in different years. SAS PROC CORR was used to calculate simple and phenotypic correlation coefficients.

Genetic correlation

Genetic correlation coefficients were estimated using midparent values and progeny means as described by Becker (1984). The correlation coefficient formula is $r_a = \frac{COV_{X1Y2} + COV_{X2Y1}}{2\sqrt{COV_{XX} COV_{YY}}}$, where COVxy is the 'cross-variance', and COVxx and COVyy are the offspring-parent covariance for each trait separately. The cross-variance is calculated from X in parents and Y in offspring [$COV(X_1, Y_2)$] as well as from Y in parents and X in offspring [$COV(X_2, Y_1)$].

Results and Discussion

The largest positive phenotypic correlation coefficients were among nut size traits (nut length, nut width, nut depth, nut weight, and kernel weight) and among phenological traits (date of opening of female flowers, time of catkin elogation, and time of leafing out) (Table 4.1), and the 1994 and 1995 data were highly correlated for each of these traits (Table 4.4). Mehlenbacher (1991) obtained similiar phenotypic correlation

Table 4.1 Phenotypic correlation coefficients between 17 traits in the OSU hazelnut breeding program[X]

	NL	NW	ND	NSI	NCI	%K	NWT	KWT	FA	BA	HL	RHL	NNPC	NM	DOFF	TCE	LO
NL		0.659**	0.622**	-0.308	-0.226	-0.374*	0.871**	0.771**	0.178	-0.163	.	.	.	.	-0.015	-0.255	-0.142
NW	0.569**		0.933**	0.497**	-0.285	-0.223	0.859**	0.865**	0.054	-0.253	.	.	.	.	-0.160	-0.417*	-0.305
ND	0.535**	0.951**		0.521**	-0.601**	-0.133	0.845**	0.894**	0.026	-0.333	.	.	.	.	-0.048	-0.449*	-0.246
NSI	-0.331*	0.572**	0.600**		-0.269	0.180	0.107	0.247	-0.142	-0.162	.	.	.	.	-0.116	-0.263	-0.199
NCI	-0.308*	-0.632**	-0.835**	-0.540**		-0.110	-0.384*	-0.490**	-0.022	0.339	.	.	.	.	-0.170	0.320	0.059
%K	-0.319*	-0.146	0.013	0.215	-0.233		-0.424*	-0.016	0.038	-0.171	.	.	.	.	-0.157	-0.146	0.007
NWT	0.778**	0.902**	0.882**	0.271	-0.630**	-0.325		0.908**	0.215	-0.234	.	.	.	.	-0.121	-0.452*	-0.341
KWT	0.657**	0.884**	0.925**	0.403**	-0.776**	0.127	0.894**		0.229	-0.372*	.	.	.	.	-0.235	-0.567**	-0.397*
FA	-0.268	-0.286	-0.226	-0.031	0.077	0.045	-0.227	-0.238		-0.224	.	.	.	.	-0.090	-0.248	-0.145
BA	0.016	-0.127	-0.219	-0.190	0.348*	-0.058	-0.183	-0.238	-0.181		.	.	.	.	0.522**	0.486*	0.454*
HL	0.490**	0.436**	0.510**	0.060	-0.512**	-0.007	0.526**	0.546**	-0.051	-0.284		.	.	.	.	.	.
RHL	-0.027	0.148	0.247	0.241	-0.382*	0.201	0.127	0.224	0.082	-0.334*	0.855**		.	.	.	.	.
NNPC	-0.214	-0.017	-0.064	0.171	0.114	-0.374*	-0.225	-0.073	-0.111	0.236	0.211	0.369*		.	.	.	.
NM	0.031	-0.002	-0.094	-0.111	0.231	-0.282	0.019	-0.093	-0.054	0.029	0.028	-0.004	0.007		.	.	.
DOFF	0.286	-0.072	-0.063	-0.340*	0.099	-0.298	0.051	-0.102	-0.030	0.484**	-0.056	-0.233	-0.213	0.044		0.571**	0.802**
TCE	-0.141	-0.430**	-0.434**	-0.369*	0.402*	-0.121	-0.407*	-0.491**	0.062	0.364*	-0.288	-0.251	-0.062	0.296	0.579**		0.692**
LO	0.112	-0.226	-0.201	-0.356*	0.170	-0.187	-0.111	-0.215	0.009	0.393*	-0.222	-0.319	-0.186	0.139	0.754**	0.630**	
	NL	NW	ND	NSI	NCI	%K	NWT	KWT	FA	BA	HL	RHL	NNPC	NM	DOFF	TCE	LO

* Significant at 0.05;
** Significant at 0.01.
X: Numbers above the diagonal line are coefficients from 1994, and these below the diagonal line are from 1995.

Table 4.2 Simple and Phenotypic correlation coefficients of 13 traits in different years[z]

Trait	Simple correlation coefficients	Phenotypic correlation coefficients
NL	0.861	0.920
NW	0.802	0.912
ND	0.855	0.948
NSI	0.810	0.918
NCI	0.729	0.888
%K	0.815	0.906
NWT	0.817	0.878
KWT	0.798	0.888
FA	0.578	0.661
BA	0.614	0.796
DOFF	0.625	0.864
TCE	0.772	0.910
LO	0.810	0.932

[z] all correlation coefficients in this table are significant at P=0.01.

coefficients for three phenological traits, including time of catkin elongation, stigma exsertion, and leaf bud swell, when 45 genotypes of *Corylus avellana* L. were used as experimental materials.

Nut shape index is a function of nut length, nut width and nut depth, while nut compression index is a function of nut width and nut depth. There were obvious correlations between nut size traits and nut shape traits. Although % kernel is the ratio of kernel weight to nut weight, there was a negative correlation between % kernel and nut weight. Positive correlation coefficients existed between blanching ability and three phenological traits (date of opening of female flowers, time of catkin elongation, and leafing out). Strong negative correlation coefficients were also observed between time of catkin elongation and nut size traits, including nut width, nut depth, nut weight and kernel weight. Although husk length was positively correlated with 5 nut size traits, correlations of relative husk length and the same size traits were much smaller. Nut compression index showed large negative correlations with nut weight and kernel weight.

Simple correlation coefficients calculated from individual seedling values (Table 4.3) were similar to phenotypic correlation coefficients calculated using progeny means, but their values were smaller and more statistically significant because of the larger number of data points.

Phenotypic correlation coefficients are functions of genetic correlation coefficients and environment correlation coefficients, but not linear combinations of both coefficients (Searle, 1961). For characters with high heritabilities, the genetic correlation is more important in determining the phenotypic correlation (Falconer and Machay, 1996). Our results showed all traits had high narrow sense heritability estimates (Chapter

Table 4.3 Simple correlation coefficients between 17 traits in the OSU hazelnut breeding program[x]

	NL	NW	ND	NSI	NCI	%K	NWT	KWT	FA	BA	HL	RHL	NNPC	NM	DOFF	TCE	LO
NL		0.444**	0.482**	-0.501**	-0.217**	-0.259**	0.713**	0.666**	0.124**	-0.123**	.	.	.	.	0.016	-0.144**	-0.029
NW	0.395**		0.898**	0.524**	-0.074	-0.325**	0.809**	0.756**	0.028	-0.130**	.	.	.	.	-0.094*	-0.185**	-0.109**
ND	0.396**	0.904**		0.479**	-0.501**	-0.228**	0.811**	0.802**	-0.007	-0.188**	.	.	.	.	-0.029	-0.224**	-0.081
NSI	-0.494**	0.574**	0.575**		-0.062	-0.032	0.120**	0.131**	-0.110**	-0.026	.	.	.	.	-0.077*	-0.067	-0.082
NCI	-0.161**	-0.215**	-0.606**	-0.263**		-0.122**	-0.257**	-0.344**	0.068	0.184**	.	.	.	.	-0.096*	0.161**	-0.002
%K	-0.256**	-0.294**	-0.172**	0.003	-0.160**		-0.449**	-0.030	0.007	-0.063	.	.	.	.	-0.137**	-0.031	-0.067
NWT	0.652**	0.818**	0.803**	0.214**	-0.313**	-0.432**		0.901**	0.140**	-0.175**	.	.	.	.	-0.049	-0.221**	-0.111**
KWT	0.666**	0.756**	0.802**	0.131**	-0.344**	-0.030	0.882**		0.145**	-0.235**	.	.	.	.	-0.128**	-0.248**	-0.165**
FA	-0.038	-0.060	-0.083*	-0.036	0.077*	0.014	-0.003	0.003		-0.041	.	.	.	.	-0.070	-0.142**	-0.027
BA	0.076*	-0.024	-0.089**	-0.112**	0.172**	-0.054	-0.065*	-0.109**	-0.135**		.	.	.	.	0.266**	0.254**	0.253**
HL	0.387**	0.335**	0.385**	0.009	-0.245**	-0.112**	0.438**	0.417**	-0.032	-0.173**		.	.	.	.	.	.
RHL	-0.208**	0.095**	0.150**	0.305**	-0.162**	0.044	0.052	0.074*	-0.013	-0.225**	0.817**		.	.	.	.	.
NNPC	-0.065*	-0.179**	-0.151**	-0.101**	0.021	0.226**	-0.230**	-0.152**	-0.087**	0.092**	0.055	0.097**		.	.	.	.
NM	0.053	0.034	-0.015	-0.042	0.096**	-0.152**	0.054	-0.009	-0.108**	0.050	0.040	-0.003	0.061		.	.	.
DOFF	0.151**	0.001	0.022	-0.120**	-0.025	-0.194**	0.066*	-0.042	0.011	0.195**	-0.019	-0.095**	-0.091**	0.008		0.433**	0.612**
TCE	-0.101**	-0.202**	-0.224**	-0.118**	0.168**	-0.016	-0.234	-0.264**	0.021	0.155**	-0.204**	-0.162**	-0.020	0.120**	0.373**		0.496**
LO	0.023	-0.070*	-0.070*	-0.091**	0.050	-0.150**	-0.011	-0.092**	0.006	0.145**	-0.154**	-0.165**	-0.175**	0.102**	0.511**	0.420**	
	NL	NW	ND	NSI	NCI	%K	NWT	KWT	FA	BA	HL	RHL	NNPC	NM	DOFF	TCE	LO

* Significant at 0.05;
** Significant at 0.01.
X: Numbers above the diagonal line are coefficients from 1994, and these below the diagonal line are from 1995.

2). Therefore, phenotypic correlation coefficients were similar in magnitude to genetic correlation (Table 4.4).

Genetic correlation can result from pleiotropy or linkage disquilibrium. It seems reasonable to assume that pleiotropy is at least partly responsible for the correlations among nut size traits as well as among phenological traits. Because our studied population includes parents of very diverse origins and few generations of crosses have been made in the program, the linkage disquilibrium might very well be responsible for many of the other significant genetic correlations.

A positive genetic correlation is not desirable when the character of interest is associated with an undesirable character (Hansche et al., 1966). On the other hand, a negative genetic correlation is not wanted when it involes two desirable characters (De Souza et al., 1998b). In the sweet cherry, Hansche et al. (1966) found there was high positive genetic correlation among the traits full bloom date, ripe date, fruit firmness and fruit diameter (0.44-0.89). Therefore, it was hard to obtain early ripening seedlings with large and firm fruit, but it was easy to obtain late blooming offspring with large and firm fruit. In the strawberry, a genetic correlation of 0.65 was found between fruit size and yield (Hansche et al., 1968), which indicated selection for yield could be expected to result in an increase in fruit size and vice versa. Hansche et al. (1972) reported a large phenotypic correlation between fruitfulness of laterals and crop size (0.41) in walnut, and recommended selection for lateral fruiting as a means to increase yield. De Souza et al. (1998a) found in their peach population that if heritability estimates were in the low to intermediate range, the genetic correlation coefficients were much higher than the

Table 4.4 Genetic correlation coefficients between 17 traits in the OSU hazelnut breeding program[X]

	NL	NW	ND	NSI	NCI	%K	NWT	KWT	FA	BA	HL	RHL	NNPC	NM	DOFF	TCE	LO
NL		0.749 (0.031)	0.746 (0.031)	-0.250 (0.115)	-0.359 (0.082)	-0.421 (0.070)	0.934 (0.009)	0.851 (0.020)	0.018 (0.112)	-0.188 (0.101)	.	.	.	.	-0.051 (0.087)	-0.355 (0.063)	-0.169 (0.072)
NW	0.731 (0.032)		0.947 (0.006)	0.445 (0.087)	-0.371 (0.072)	-0.231 (0.071)	0.897 (0.012)	0.934 (0.008)	-0.040 (0.099)	-0.371 (0.080)	.	.	.	.	-0.070 (0.077)	-0.514 (0.047)	-0.265 (0.061)
ND	0.685 (0.033)	0.933 (0.007)		0.431 (0.087)	-0.650 (0.047)	-0.152 (0.073)	0.878 (0.013)	0.946 (0.007)	-0.110 (0.097)	-0.403 (0.077)	.	.	.	.	0.094 (0.076)	-0.507 (0.047)	-0.192 (0.063)
NSI	-0.222 (0.093)	0.525 (0.067)	0.570 (0.056)		-0.237 (0.137)	0.248 (0.124)	0.056 (0.103)	0.239 (0.107)	-0.120 (0.171)	-0.281 (0.149)	.	.	.	.	0.112 (0.134)	-0.259 (0.104)	-0.141 (0.113)
NCI	-0.406 (0.060)	-0.640 (0.040)	-0.830 (0.019)	-0.510 (0.071)		-0.116 (0.100)	-0.414 (0.066)	-0.527 (0.063)	0.167 (0.130)	0.357 (0.109)	.	.	.	.	-0.386 (0.089)	0.287 (0.079)	0.018 (0.089)
%K	-0.298 (0.069)	-0.018 (0.072)	0.072 (0.064)	0.396 (0.087)	-0.286 (0.069)		-0.516 (0.053)	-0.146 (0.078)	0.086 (0.120)	-0.143 (0.111)	.	.	.	.	-0.059 (0.094)	-0.005 (0.078)	0.092 (0.080)
NWT	0.943 (0.008)	0.880 (0.015)	0.846 (0.017)	0.074 (0.092)	-0.576 (0.045)	-0.340 (0.064)		0.923 (0.009)	0.070 (0.094)	-0.349 (0.078)	.	.	.	.	-0.088 (0.074)	-0.522 (0.044)	-0.337 (0.056)
KWT	0.875 (0.017)	0.942 (0.008)	0.939 (0.007)	0.267 (0.092)	-0.732 (0.034)	0.024 (0.077)	0.916 (0.011)		0.083 (0.104)	-0.509 (0.072)	.	.	.	.	-0.161 (0.079)	-0.629 (0.041)	-0.376 (0.060)
FA	-0.232 (0.102)	-0.261 (0.095)	-0.260 (0.086)	-0.133 (0.144)	0.179 (0.103)	0.142 (0.112)	-0.145 (0.101)	-0.138 (0.108)		-0.209 (0.142)	.	.	.	.	-0.208 (0.115)	-0.327 (0.091)	-0.151 (0.103)
BA	-0.052 (0.078)	-0.153 (0.071)	-0.231 (0.062)	-0.174 (0.102)	0.383 (0.065)	0.053 (0.082)	-0.071 (0.074)	-0.139 (0.078)	-0.183 (0.112)		.	.	.	.	0.728 (0.055)	0.609 (0.060)	0.673 (0.054)
HL	0.579 (0.043)	0.454 (0.048)	0.561 (0.037)	-0.030 (0.087)	-0.669 (0.035)	-0.044 (0.068)	0.485 (0.047)	0.525 (0.047)	0.266 (0.090)	-0.300 (0.063)		.	.	.	.	.	.
RHL	0.026 (0.055)	0.087 (0.047)	0.233 (0.078)	0.128 (0.043)	-0.512 (0.061)	0.160 (0.056)	0.047 (0.059)	0.132 (0.071)	0.439 (0.056)	-0.340 (0.053)	0.000		.	.	.	.	.
NNPC	-0.118 (0.084)	0.048 (0.076)	0.001 (0.118)	0.153 (0.088)	0.040 (0.070)	0.501 (0.085)	-0.060 (0.085)	0.061 (0.123)	0.284 (0.096)	0.073 (0.069)	0.369 (0.055)	0.497		.	.	.	.
NM	0.059 (0.081)	0.099 (0.075)	-0.053 (0.069)	-0.081 (0.109)	0.336 (0.071)	-0.262 (0.080)	0.058 (0.077)	-0.025 (0.082)	-0.223 (0.115)	-0.009 (0.087)	-0.048 (0.072)	-0.101 (0.065)	-0.092 (0.099)		.	.	.
DOFF	0.282 (0.073)	-0.008 (0.075)	0.029 (0.068)	-0.370 (0.093)	-0.016 (0.079)	-0.230 (0.080)	0.198 (0.073)	0.081 (0.081)	-0.030 (0.119)	0.546 (0.060)	-0.093 (0.071)	-0.258 (0.061)	-0.320 (0.088)	-0.135 (0.088)		0.582 (0.053)	0.879 (0.019)
TCE	-0.267 (0.068)	-0.515 (0.051)	-0.508 (0.046)	-0.424 (0.081)	0.466 (0.057)	-0.072 (0.077)	-0.376 (0.060)	-0.481 (0.057)	0.001 (0.110)	0.442 (0.064)	-0.395 (0.055)	-0.327 (0.053)	-0.297 (0.083)	0.171 (0.080)	0.657 (0.046)		0.725 (0.032)
LO	-0.048 (0.057)	-0.261 (0.051)	-0.264 (0.074)	-0.396 (0.057)	0.316 (0.067)	-0.119 (0.060)	-0.145 (0.062)	-0.236 (0.094)	-0.164 (0.047)	0.570 (0.046)	-0.298 (0.053)	-0.350 (0.046)	-0.278 (0.074)	0.148 (0.071)	0.836 (0.022)	0.851 (0.018)	
	NL	NW	ND	NSI	NCI	%K	NWT	KWT	FA	BA	HL	RHL	NNPC	NM	DOFF	TCE	LO

X: Numbers above the diagonal line are coefficients from 1994, and those below the diagonal line are from 1995.

corresponding phenotypic correlation coefficients. In the peach population of De Souza et al. (1998b), there was a high positive genetic correlation coefficient between ripening date and soluble solids (0.63). Therefore, it would be hard to get offspring with early ripening and high soluble solids in this population.

For our target traits, nut maturity had no genetic correlation with most other traits. Only significant correlation existed between nut maturity and nut compression index (0.336±0.071) and between nut maturity and %K (-0.262±0.080). Similarly, %K had no genetic correlation with most other traits. There were lower genetic correlation coefficients of %K with nut length, nut shape index and nut compression index. Blanching ability only had high genetic correlation coefficients with date of opening of female flowers, time of catkin elongation, and time of leafing out. There were low genetic correlation coefficients between blanching ability with nut depth, and nut compression index. Selection of round nuts of medium size with high % kernel, easily-blanched kernels and early nut maturity can produce rapid genetic progress for all 5 traits simultaneously.

Phenotypic and simple correlation coefficients may help breeders to evaluate target traits by other traits to some extent in the offspring. Hansche et al. (1972) found phenotypic correlation coefficients of nut weight with nut length, suture, and cheek were 0.62, 0.72, and 0.78 in walnut and thought an improvement in the overall efficiency of the breeding program could probably be acheived by diverting the resources required to measure nut weight and size to increasing the sample size from which kernel traits were estimated. In our experiments, nut size measurements were also correlated with each other and thus somewhat redundant (Fig. 4.1).

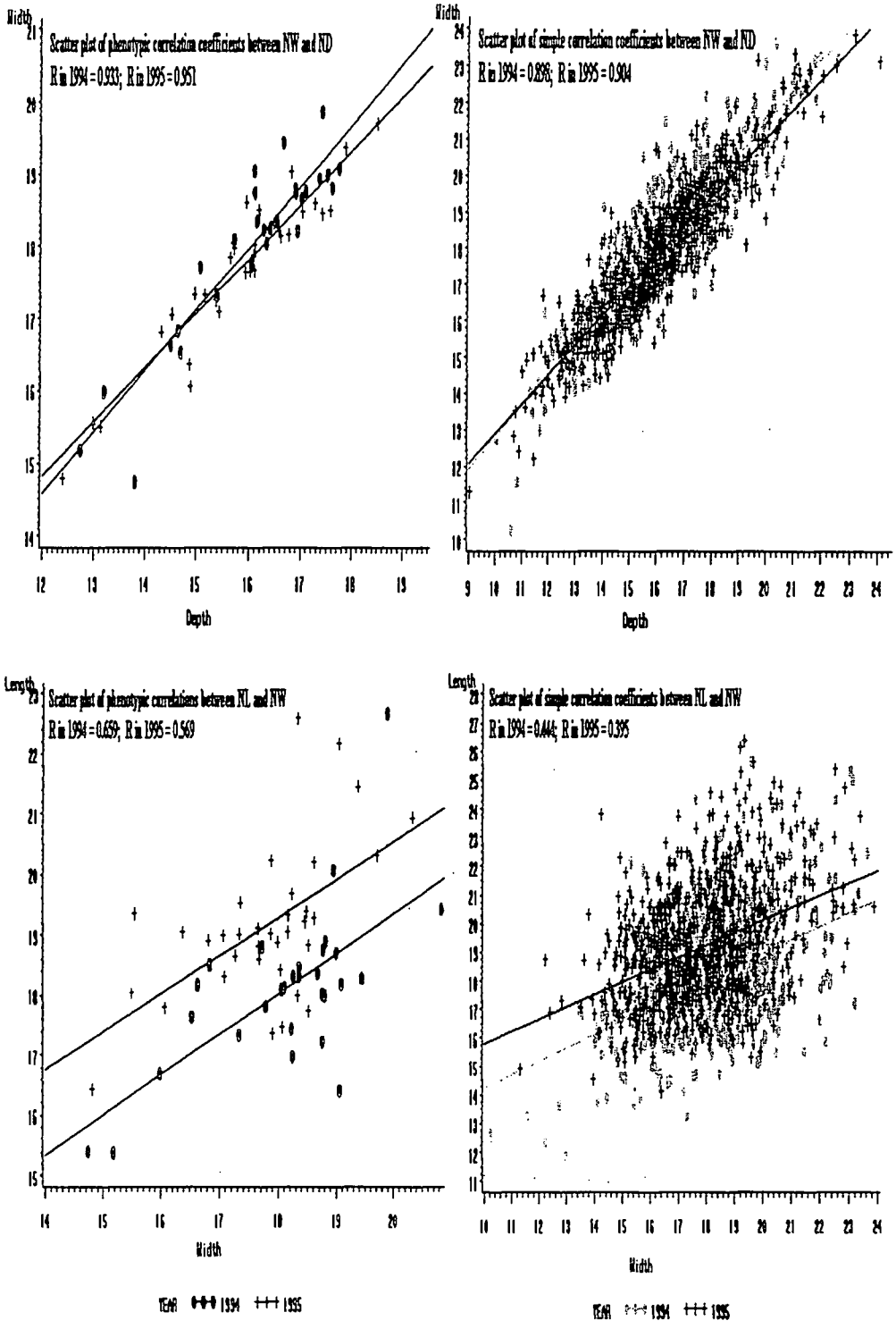

Figure 4.1 Scatter plot of the strongest phenotypic and simple correlation coefficients

In the OSU hazelnut breeding program, there were no specific requirements for the improvement of TCE, DOFF and LO, except for elimination of nondormant types (very early LO) (Mehlenbacher, 1994). Therefore, these three phenological traits might be useful in pre-selecting seedlings for the improvement of blanching ability.

The phenotypic correlation coefficients of blanching ability with TCE, DOFF and LO were 0.364, 0.484 and 0.393 respectively, but the simple correlation coefficients between them were only 0.155, 0.195 and 0.145 respectively. Late individuals (TCE ≥9, DOFF≥9, or LO≥6) did not blanch well. This is because the easily blanched parents in this study are from Turkey, Italy, and Spain and typically have low scores for phenological traits.

Correlation coefficients for the same trait measured on the same genotypes in different environments may reflect G x E interaction (Cooper, et al., 1994). As G x E interaction has a stronger influence (Falconer, 1989), correlation coefficients decrease. Our results showed that the 1994 and 1995 measurements for all traits were highly correlated (Table 4.2). These high values indicate that genotype by year interaction is small and are consistent with the results from estimation of variance components (Chapter 3). Simple correlation coefficients were based on individual seedling values, which had larger genotype x year interaction than family means. Simple correlation coefficients are lower than phenotypic correlation coefficients.

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CHAPTER 5

DISTRIBUTION OF 17 QUANTITATIVE TRAITS IN HAZELNUT PROGENIES

Abstract

The distribution of 17 quantitative traits was studied in 35 hazelnut *(Corylus avellana* L.) progenies using histograms. All 13 nut and kernel traits and 4 phenological traits showed continuous distributions. Most approximated normal distributions, except number of nuts per cluster, which was skewed toward lower values. Progeny means were very similiar to midparent values. Transgressive segregation was common except when parents had very different values. Bimodal distributions for time of catkin elongation and date of opening of female flowers are attributed to lack of development during periods of cold temperature.

Introduction

Hazelnut is an important nut crop in Oregon. The Oregon State University hazelnut breeding program is developing improved varieties for the kernel market. The specific objectives were listed by Mehlenbacher (1994): i) resistance to big bud mite; ii) round nuts with medium size; iii) high % kernel; iv) precocity and high yield; v) easily blanched kernels; vi) few nut and kernel defects; vii) early maturity; and viii) free-falling nuts. Eastern filbert blight caused by *Anisogramma anomala* (Peck) E. Müller is a serious threat to the industry, and the development of resistant or immune varieties to this

disease is also an objective (Coyne et al., 1998; Johnson et al., 1996; Osterbauer et al., 1997).

The heritability in the narrow sense of 22 quantitative traits has been examined to date, including 8 kernel and nut defects (Mehlenbacher et al., 1993), 9 nut and kernel traits (Romisondo et al., 1983; Thompson, 1977b), 3 measurements of disease susceptibility (Osterbauer et al., 1997), susceptibility to big bud mites (Thompson, 1977a) and date of budbreak (Thompson et al., 1996), there is still little information available on the distribution of traits in progenies from controlled crosses for most traits of interest. This paper presents and discusses the distribution of 17 traits in 35 hazelnut progenies.

Materials and Methods

Seventy seven trees representing 41 genotypes (1-2 trees of each of 23 cultivars and 18 selections) were used to estimate parent values, and 35 progenies from controlled crosses were examined (Table 5.1). 17 traits, including 13 nut and kernel traits and 4 phenological traits, were investigated. Each cross consisted of 18-31 seedlings. The data were from observations recorded between August, 1995 and April, 1996. The detailed information was described in Chapter 2.

The observational standards and evaluation methods of 17 traits were described in Chapter 2. Histograms are used to show distributions of all traits. Frequencies are presented as percentages. Histograms show the distributions in the pooled sample of all seedlings and in each of the 35 progenies for each of the 17 traits with tree means.

Table 5.1 Code number and parents for 35 crosses

Parents of crosses	Code number	P1	P2
183.060 x VR 20-11	440	183.060	VR 20-11
Willamette x 054.021	444	Willamette	54.021
055.077 X Sant Jaume	445	55.077	Sant Jaume
186.080 x VR 17-15	446	186.080	VR 17-15
Fusco Rubra X Hall's Giant	4510	Fusco Rubra	Hall's Giant
Fusco Rubra x Romisondo G1	4511	Fusco Rubra	Romisondo G1
Fusco Rubra x Casina	4512	Fusco Rubra	Casina
Contorta x Aurea	453	Contorta	Aurea
Negret x Tonda di Giffoni	454	Negret	Tonda di Giffoni
TGDL x Gem	455	TGDL	Gem
Willamette x Segorbe	4560	Willamette	Segorbe
Negret x 225.077	4561	Negret	225.077
Ribet x Willamette	457	Ribet	Willamette
TGDL x 054.039	458	TGDL	54.039
023.017 x GH 088.014	463	23.017	GH 088.014
Willamette x Hall's Giant	4650	Willamette	Hall's Giant
166.034 x Hall's Giant	4651	166.034	Hall's Giant
Casina x Mortarella	468	Casina	Mortarella
Romisondo G1 x 055.129	4710	Romisondo G1	55.129
255.003 x 055.129	4711	255.003	55.129
Tonda di Giffoni x 179.043	473	Tonda di Giffoni	179.043
162.017 x Birk 005-006	475	162.017	Birk 005-006
255.003 x Tonda di Giffoni	4760	255.003	Tonda di Giffoni
244.001 x Tonda Romana	4761	244.001	Tonda Romana
245.094 x Negret	480	245.094	Negret
245.094 x 179.043	481	245.094	179.043
Casina x Brixnut	484	Casina	Brixnut
Ribet x 039.044	485	Ribet	39.044
246.128 x Contorta	486	246.128	Contorta
23.017 x VR 020-010	489	23.017	VR 20-11
Willamette x 026.072	490	Willamette	26.072
Negret x Segorbe	5050	Negret	Segorbe
GH 140.004 x Birk 005.006	5051	GH 140.004	Birk 005.006
Negret x 054.039	511	Negret	54.039
233.007 x Daviana	520	233.007	Daviana

Results and Discussion

All traits showed continuous distributions and most traits had approximately normal distributions when data from all offspring were pooled (Fig. 5.1). However, the distribution of number of nuts per cluster was skewed toward lower numbers. Time of catkin elongation and date of opening of female flowers had bimodal distributions. The missing values (week 8 for DOFF is the same as week 11 for TCE) corresponded to a period of cold weather from January 30, 1996 to February 5, 1996 (http://www.ocs.orst.edu/pub_ftp/climate_data/daily/ temp/temp1862.dly). Fiber amount had a narrow rating scale (1-4) (Thompson et al., 1978). Its distribution was not normal.

Because the sample from each cross for each of 17 traits in our study was very small (18-31 seedlings) compared with the pooled data, many non-normal distributions can be seen. However, continuous distributions still existed in all the individual families for all studied traits except TCE and DOFF. This kind of continuous variation is thought to be due to the action of a number of genes whose expression in the phenotype is cumulative and there are no major gene effects (Falconer, 1981). Stephen et al. (1995) , and Crane and Lewis (1949) respectively had similar reports on inheritance of ripening date of apple and inheritance of pear fruit traits, including fruit shape, fruit size, fruit length, fruit surface, and ripening date.

Bi- and tri-modal distributions for ripening date have been observed in some crosses in peach. This was attributed to the segregation at a few major genes which controlled ripening date (Bailey and Hough, 1959; Bassi et al., 1989; French, 1951). All traits had high heritability (Chapter 2), and it was expected that progeny means would be near mid-parent values. Hazelnut genotypes are highly heterozygous, and transgressive

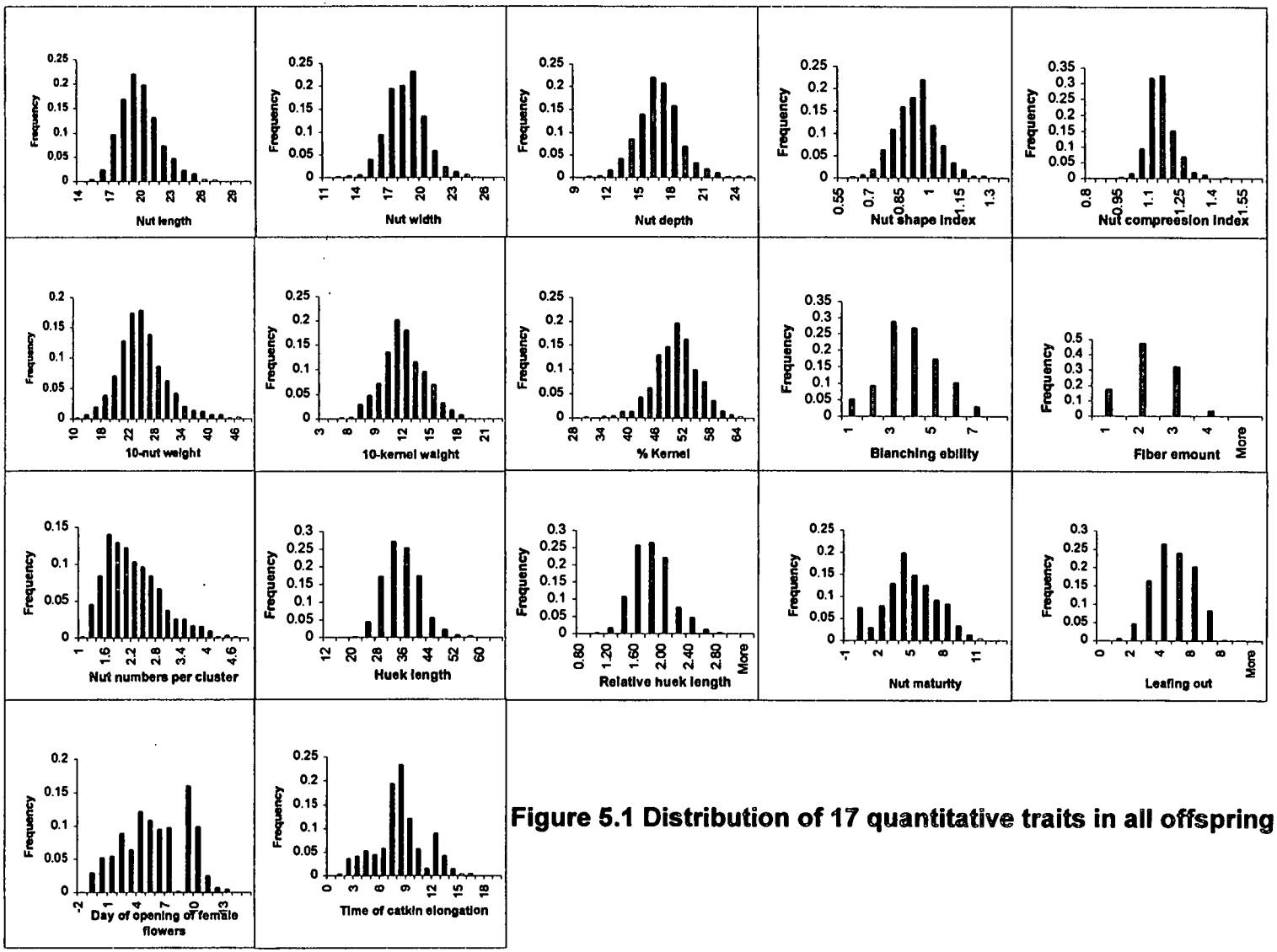

Figure 5.1 Distribution of 17 quantitative traits in all offspring

segregation was expected in the progenies. Therefore, a hazelnut breeder can make parent combinations for the improvement of target traits based on midparent values. Of course, for a specific trait, there probably are some specific suggestions for parent combinations.

Nut length, nut width and nut depth

Nut length, nut width and nut depth are measures of nut size. Nut size is an important trait for both in-shell and kernel markets because nut size reflects kernel size if there is no serious kernel shrinkage. The world kernel market needs kernels 11-13 mm in diameter. In this population, nut length showed a distribution slightly skewed toward smaller nuts (Fig. 5.1). Nevertheless, there were 21 crosses whose progeny means were between the two parent values, 13 crosses whose progeny means were slightly smaller than the smaller of the two parents, and only one cross whose progeny mean was slightly larger than the larger parent value. Transgressive segregation was common when parents had nuts of nearly identical length (Fig. 5.2), but no transgressive segregation was seen when parents differed in nut length by more than 6 mm.

When the two parent values for nut width were nearly identical, transgressive segregation for larger and smaller nuts was observed (Fig. 5.3). When the difference between the two parent values was larger than 3.5mm, transgressive segregation was very rare, or only transgressive segregation toward one side was observed. In the population, the progeny means in 16 crosses were smaller than the narrower parent, and only one progeny mean had a larger value than the wider parent.

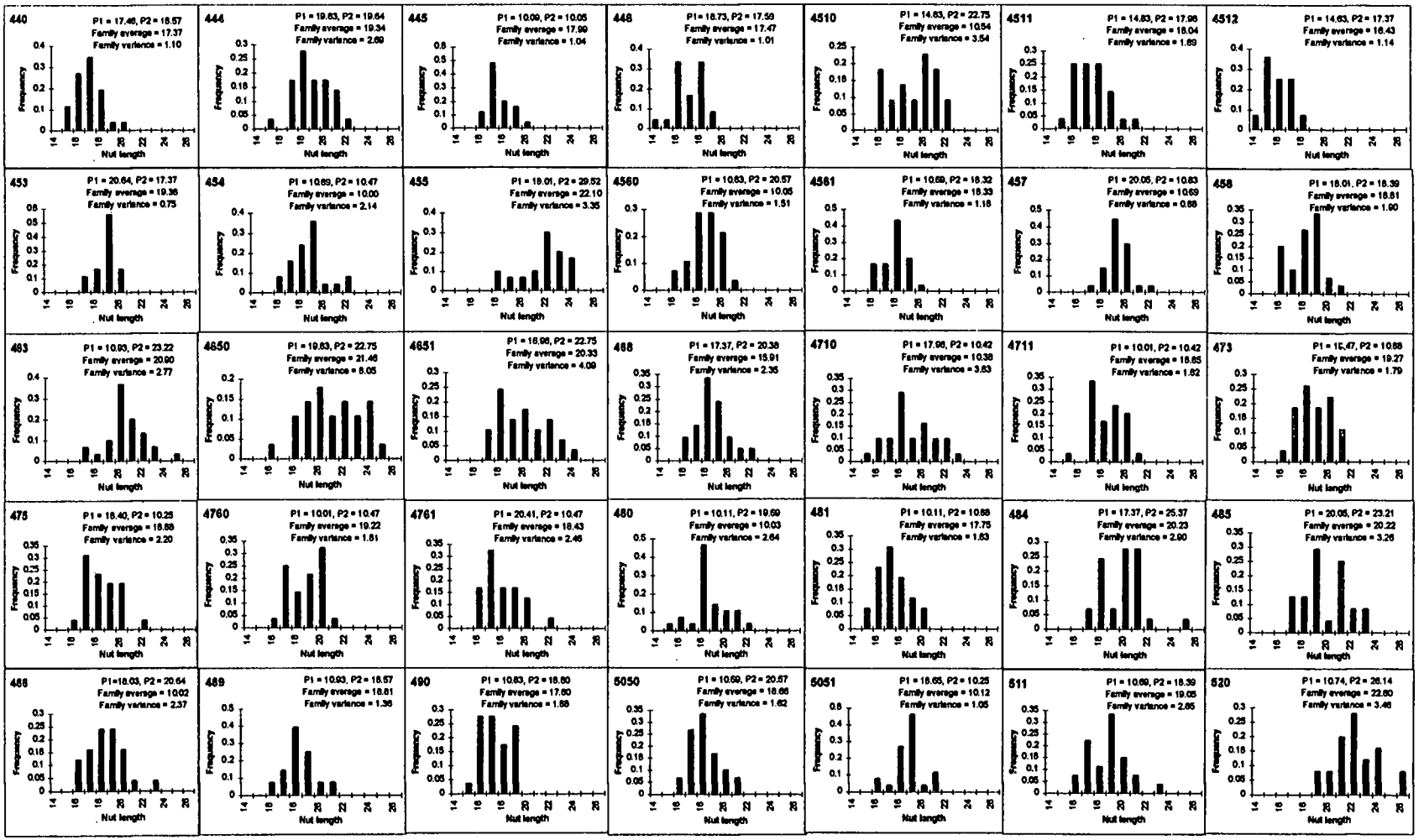

Figure 5.2 Distribution of nut length in the offspring of 35 crosses

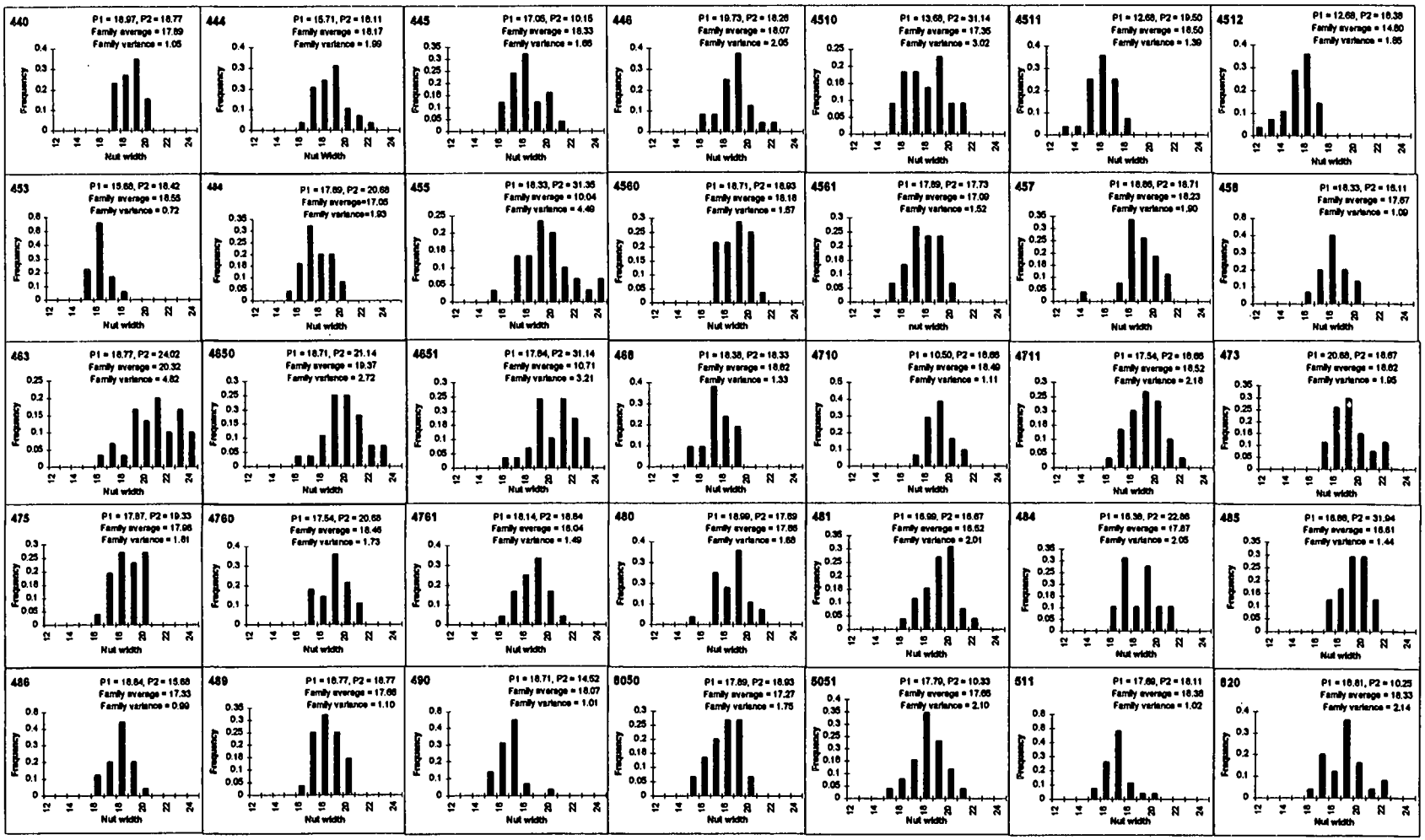

Figure 5.3 Distribution of nut width in the offspring of 35 crosses

Nut depth showed wide transgressive segregation in progenies too (Fig. 5.4). When the difference in nut depth between the two parents was more than 4.5 mm, there was little transgressive segregation. The progeny means in 14 families were slightly smaller than the smaller parent. Only one progeny had a value greater than the larger parent.

Nut shape index and compression index

Two indexes are used to quantify nut shape (Mehlenbacher 1991a). The shape index is 0.50-0.89 for long nuts, 0.90-1.00 for round nuts, and 1.01-1.30 for oblate nuts. The compression index reflects the degree of nut compression. The value of the compression index is 1.00-1.15 for round nuts and greater than 1.15 for compressed nuts. When a cross between parents with long nuts was made, long nuts predominated in the offspring, and oblate nuts were almost never observed. When crosses were made between a parent with long nuts and a parent with round nuts, seedlings with long nuts and round nuts co-existed and there were a few oblate nuts. When crosses were made between a parent with long nuts and a parent with oblate nuts, long nuts and round nuts predominated in the offspring. When a cross of two parents with round nuts was made, all three types of nuts were present in the offspring.

When crosses were made between a parent with long nuts and a parent with oblate nuts, round nuts predominated in the offspring, but long nuts and oblate nuts were still observed. No oblate X oblate crosses were studied. Based on these results, we suggest that for the improvement of nut shape, at least one parent have round nuts. Oblate X long crosses are an alternative.

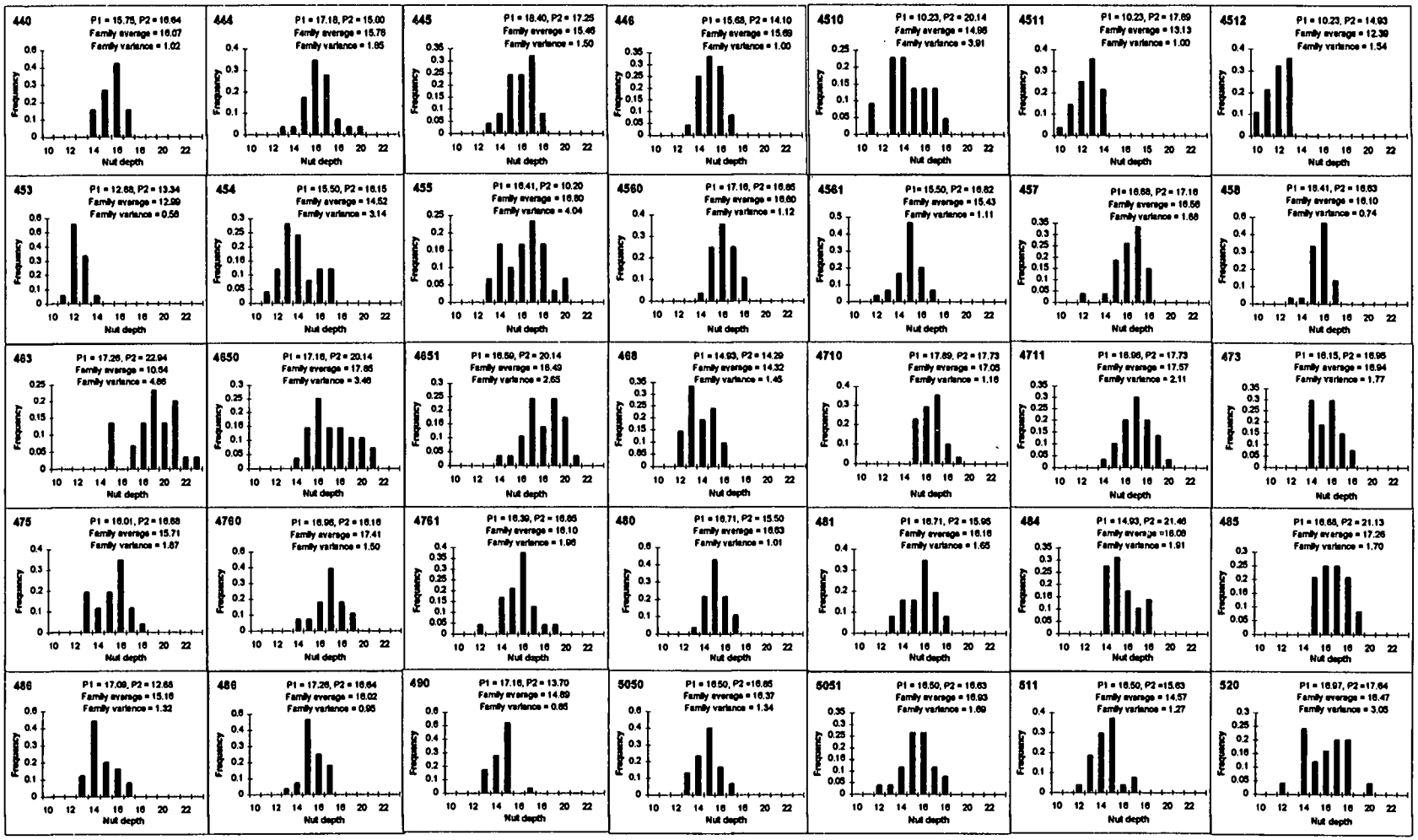

Figure 5.4 Distribution of nut depth in the offspring of 35 crosses

For shape index, there were 10 crosses whose progeny means were very slightly smaller than the parent with the smaller value, and four crosses whose progeny means were slightly larger than the parent with the larger value (Fig. 5.5). All crosses showed transgressive segregation except cross 486 (OSU 246.128 X Contorta) because the two parents of this cross had a large difference in shape index.

Similarly, transgressive segregation for compression index was observed in most crosses. Progeny means in four crosses were very slightly smaller (less compressed) than the parent with the smaller value, and progeny means in five crosses were very slightly larger than the parent with larger value (Fig. 5.6).

% Kernel, nut weight and kernel weight

When well-filled nuts are used, % kernel is a function of shell thinness. If one parent was less than 40% kernel, very few seedlings exceeded 52% kernel. Thompson (1977b) stated that 50% kernel or greater was desirable. If we accept this as the cutoff value, the frequency of desirable seedlings depends on the parent combinations. Crosses "4510", "453", and "455" were undesirable for the improvement of % kernel. When two cultivars with thin shells were crossed, there was a high frequency of seedlings with thin shells, and % kernel more than 60 often occurred. All 35 crosses showed transgressive segregation (Fig. 5.7). There were six crosses whose progeny means were slightly lower than the lower parent, and seven crosses whose progeny means were slightly higher than the high parent.

Nut weight is a function of shell thickness and kernel weight. Most crosses showed transgressive segregation toward lighter nut weight. There were 10 crosses

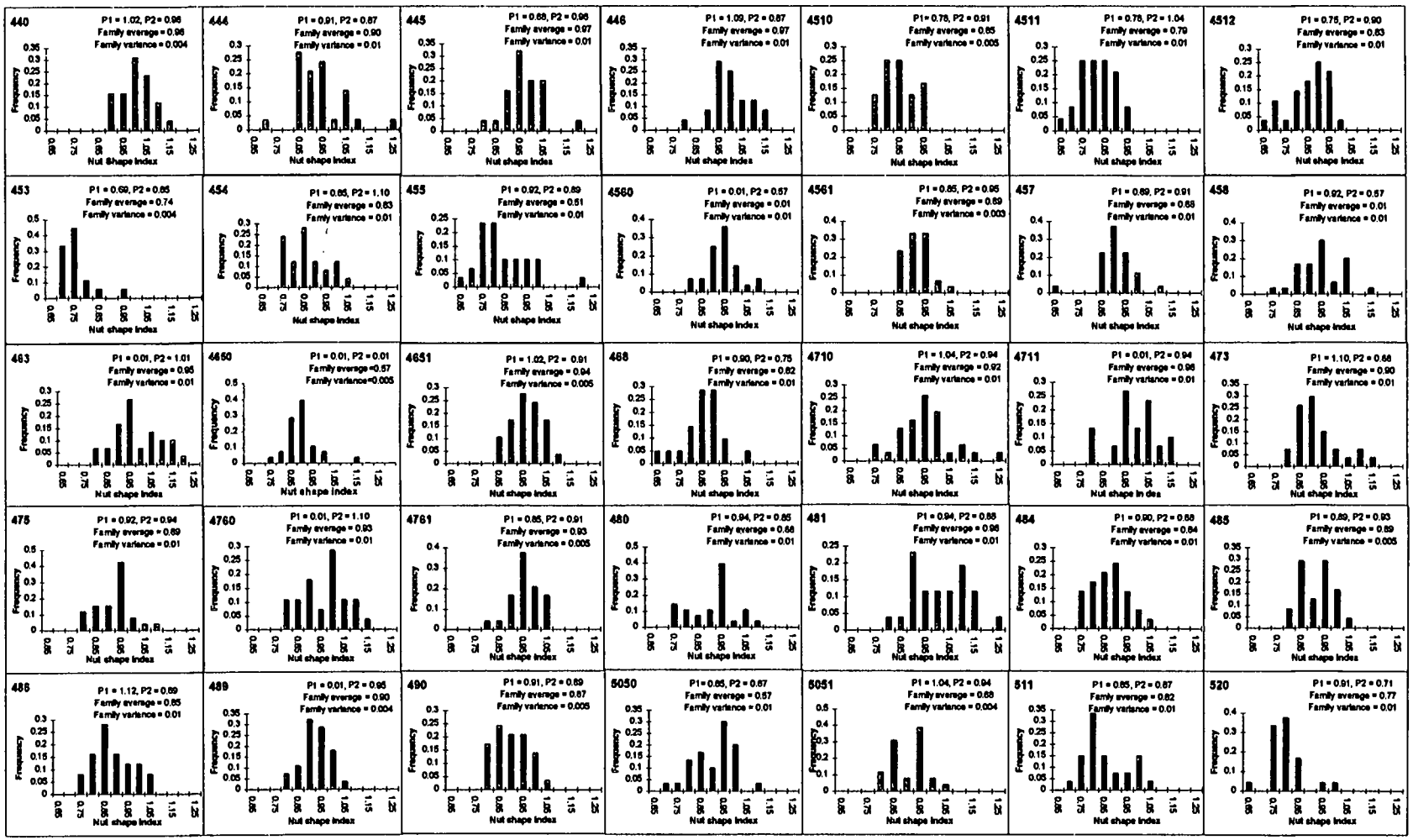

Figure 5.5 Distribution of nut shape index in the offspring of 35 crosses

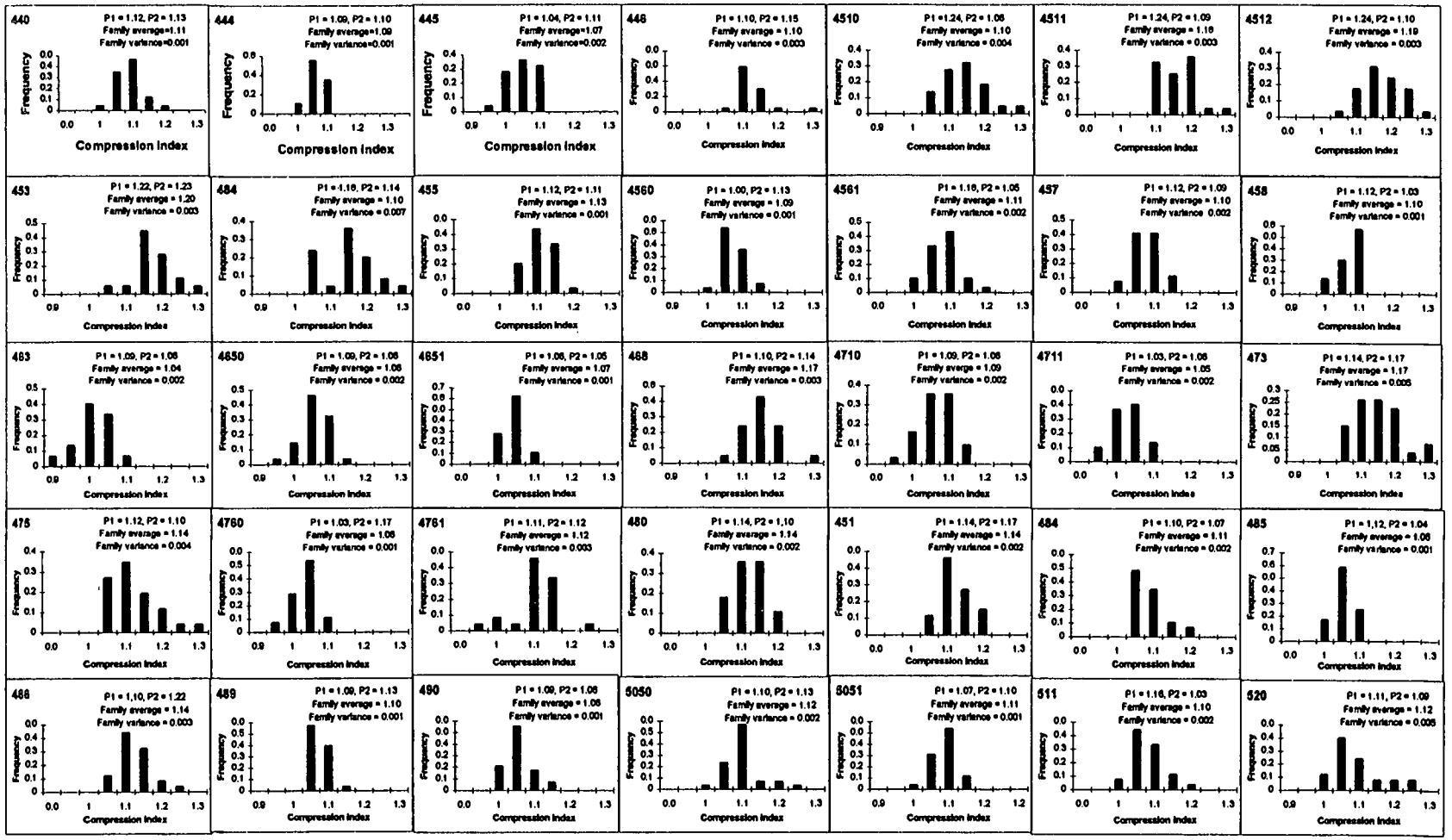

Figure 5.6 Distribution of nut compression index in the offspring of 35 crosses

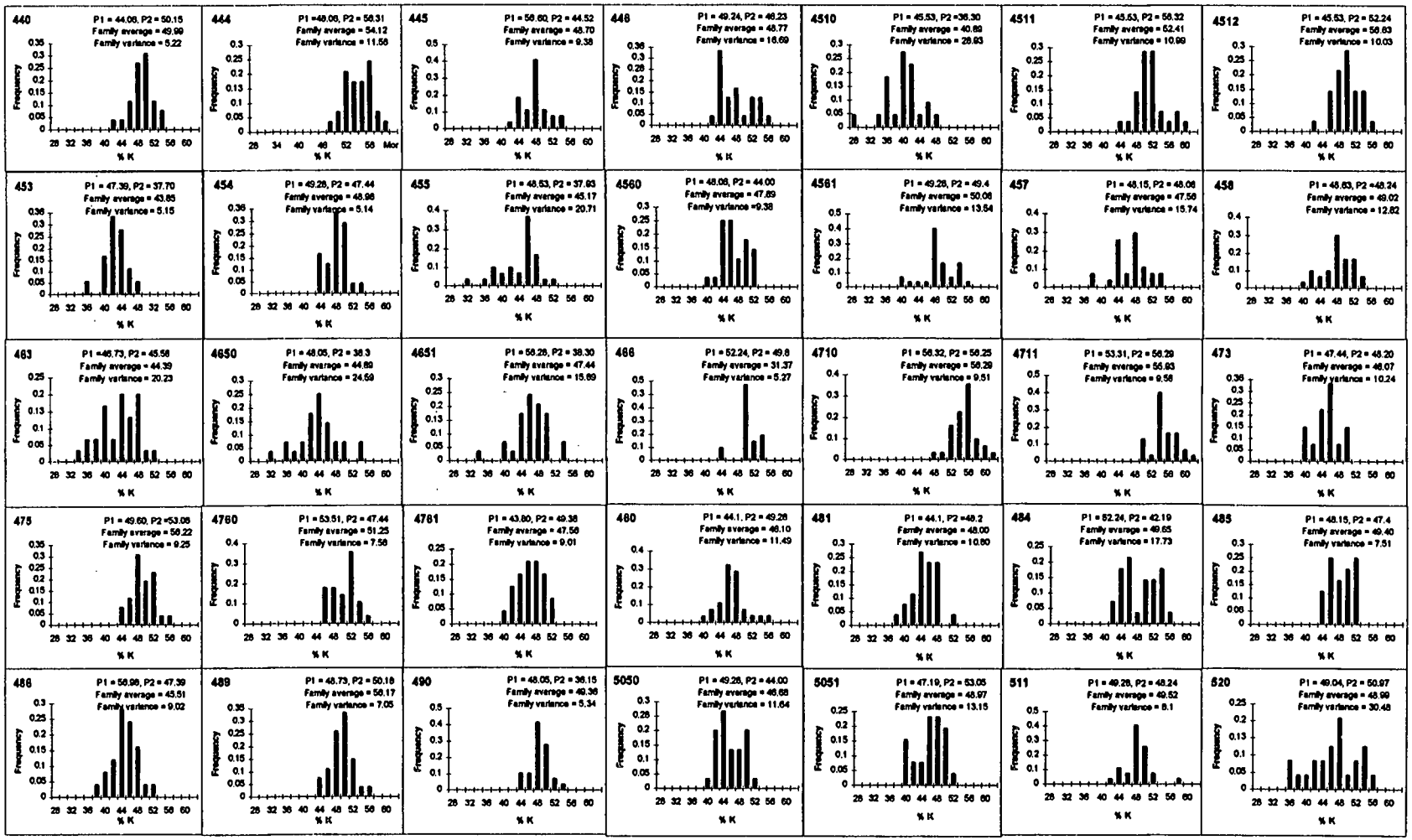

Figure 5.7 Distribution of % Kernel in the offspring of 35 crosses

whose progeny means were smaller than the smaller parent, and only one cross whose progeny mean was larger than the larger parent (Fig. 5.8).

Kernel weight also indicates kernel size and is a numerator of % K. Desirable kernel weight is between 1.3-1.7 g/kernel. Transgressive segregation was very common, especially toward lighter kernels unless the difference between the two parent values was more than 6 g. There were 11 crosses whose progeny means were slightly smaller than the parent with lighter kernels, and only one cross whose progeny mean was slightly larger than the parent with heavier kernels (Fig. 5.9).

Blanching ability

Blanching ability is an important trait for the blanched kernel market. The OSU hazelnut breeding program set 'Barcelona' as the minimum standard and 'Negret' as the ideal standard for the improvement of blanching ability (Mehlenbacher, 1995). Based on Thompson's criterion (Thompson et al., 1978), selections should have blanching ratings less than or equal to 4. When the blanching ability of a parent was greater than or equal to 5, no offspring with complete removal of pellicle (rating = 1) occurred even though blanching ability of the other parent was equal to or was close to 1. When blanching ability of the two parents was both more than or equal to 4, less than 10% of the progeny blanched well (less than or equal to 3). Although progeny means for blanching ability were around mid-parent values, there were still 11 crosses whose progeny means were higher than the higher parent, and 2 crosses whose progeny means were lower than the lower parent. Transgressive segregation existed in all crosses, especially toward poor

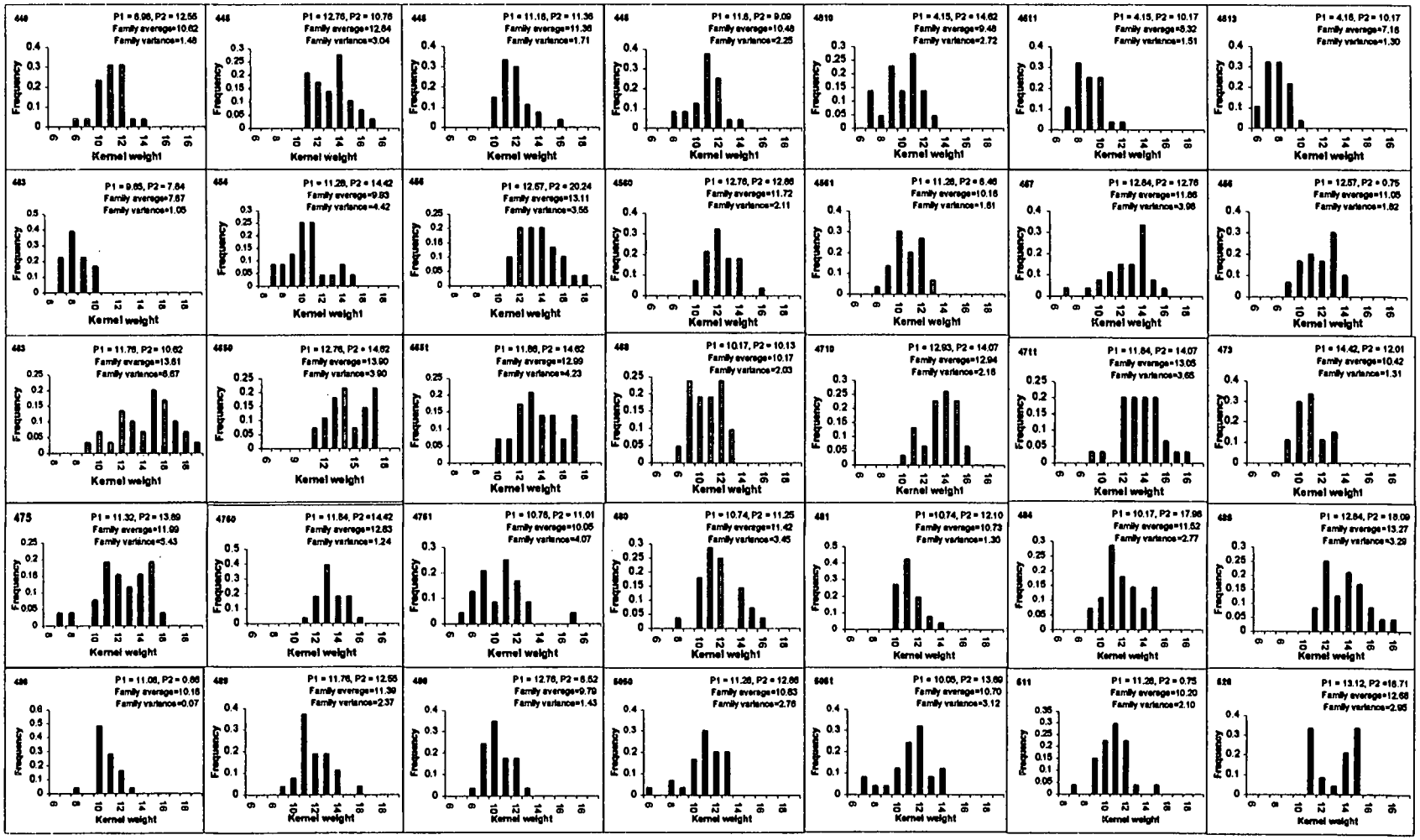

Figure 5.9 Distribution of kernel weight in the offspring of 35 crosses

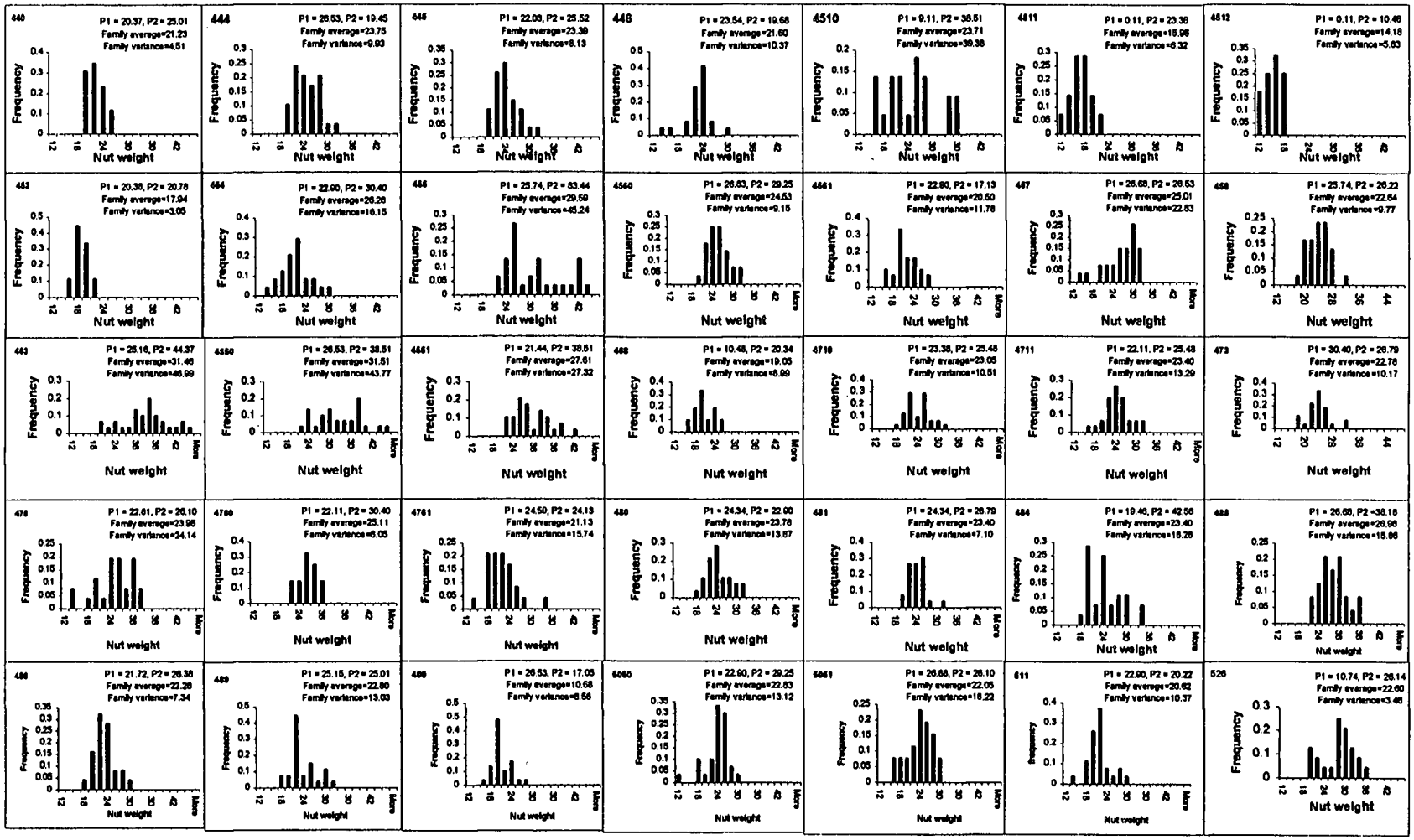

Figure 5.8 Distribution of nut weight in the offspring of 35 crosses

blanching ability (Fig. 5.10). This suggests that if the improvement of blanching ability is a priority, both parents should blanch easily.

Fiber amount

Fiber amount is an important trait for the unblanched kernel and in-shell markets. For the blanched kernel market, this trait is unimportant as fiber is removed in the blanching process. Because this trait is evaluated using a scale with only 4 classes, wide segregation was not observed in the offspring. Nevertheless, there was transgressive segregation in almost all crosses, and a high frequency of kernels heavily covered with fibrous material. There were 10 crosses whose progeny means were higher than the higher parent, and only two crosses whose progeny means were lower than the lower parent (Fig. 5.11).

Number of nuts per cluster

Number of nuts per cluster is a trait which affects yield as well as nut shape. For heavy crops it is desirable to have several nuts per cluster. However, too many nuts in a cluster may cause reduced nut size and irregular shapes due to pressure of the developing nuts on each other (Thompson, 1977b). Three to four nuts per cluster was considered optimum. Thompson (1977b) evaluated this trait using a rating scale and found it to have low heritability, but we used actual measurements to evaluate the trait, and found it to be highly heritable in our population. Although all crosses produced some offspring with more than 2 nuts per cluster, only crosses with mid-parent values greater than 1.7 gave more than 20% of seedlings with more than 2 nuts per cluster. In the crosses "454"

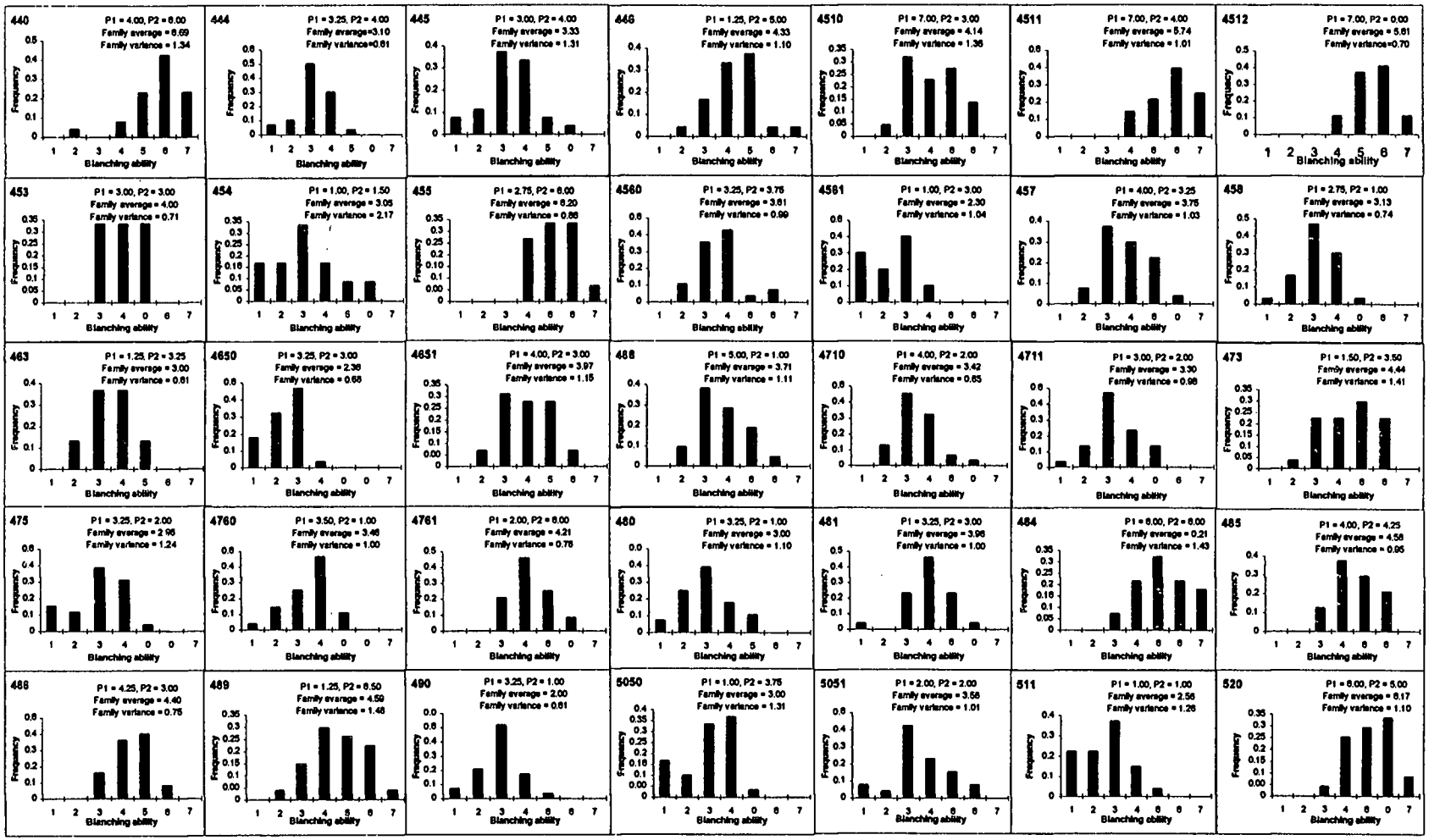

Figure 5.10 Distribution of blanching ability in the offspring of 35 crosses

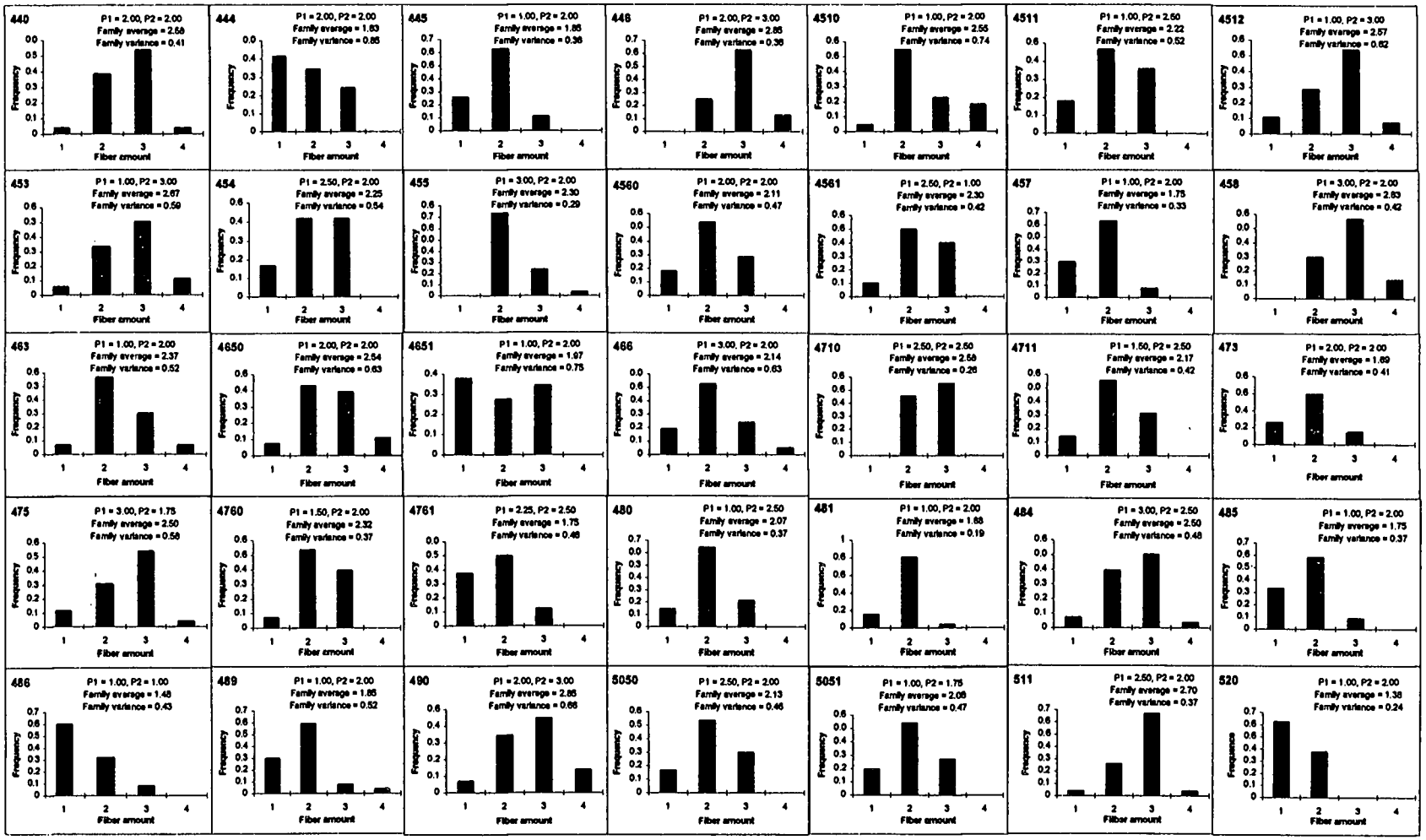

Figure 5.11 Distribution of fiber amount in the offspring of 35 crosses

('Negret' X 'Tonda di Giffoni') and "485" ('Ribet' X '039.044'), even though their mid-parent values were 1.96 and 1.87 respectively, the frequency of seedlings with desirable nut numbers per cluster in the offspring was still lower than 10%. As expected, the progeny means for most crosses were around the mid-parent values. There were 6 crosses whose progeny means were slightly higher than the higher parent, and 5 crosses whose progeny means were slightly lower than the lower parent (Fig. 5.12).

Husk length

Husk length is a trait which affects the ability of nuts to fall free of the husk at maturity. Free-falling nuts are essential in Oregon because nuts are mechanically harvested from the ground. Although other factors affect the ability of nuts to fall free of the husk, such as adhesion of the base of the nut to the husk, and degree of constriction of the husk beyond the nut, husk length is an important component. Thompson (1977b) noted husk length relative to nut length and found the heritability of this trait to be low. When we used actual measurements of husk length, we obtained a high heritability estimate in our population (Chapter 2). Transgressive segregation was very common, especially toward shorter husk length. Only four crosses ["4510" ('Fusco Rubra' X 'Hall's Giant'), "4512" ('Fusco Rubra' X 'Casina'), "489" ('023.017' X 'VR20.10') and "511" ('Negret' X '054.039')] had few or no transgressive segregates due to the large difference in husk length between the two parents. There were 15 crosses whose progeny means were shorter than the two parent values (Fig. 5.13).

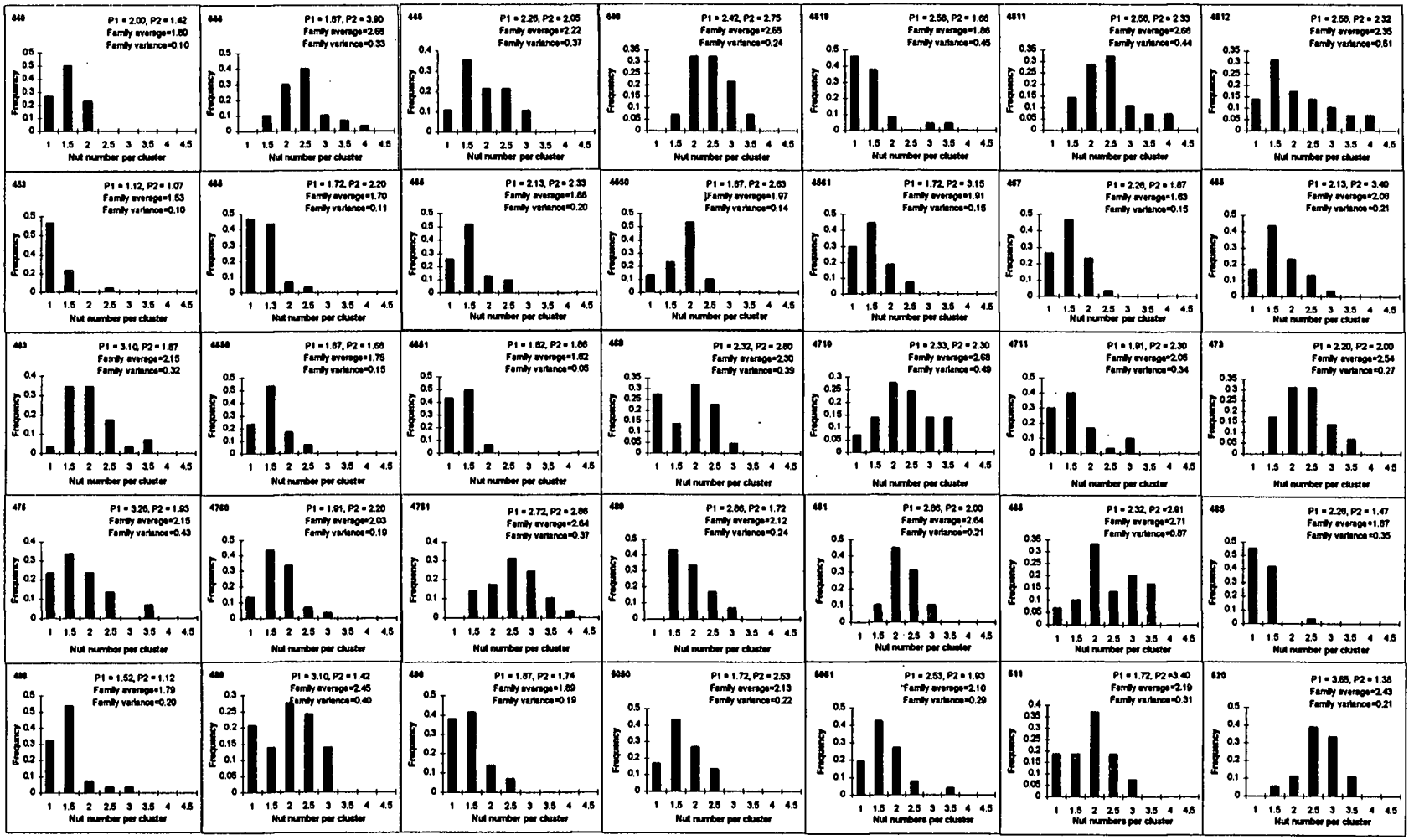

Figure 5.12 Distribution of nut number per cluster in the offspring of 35 crosses

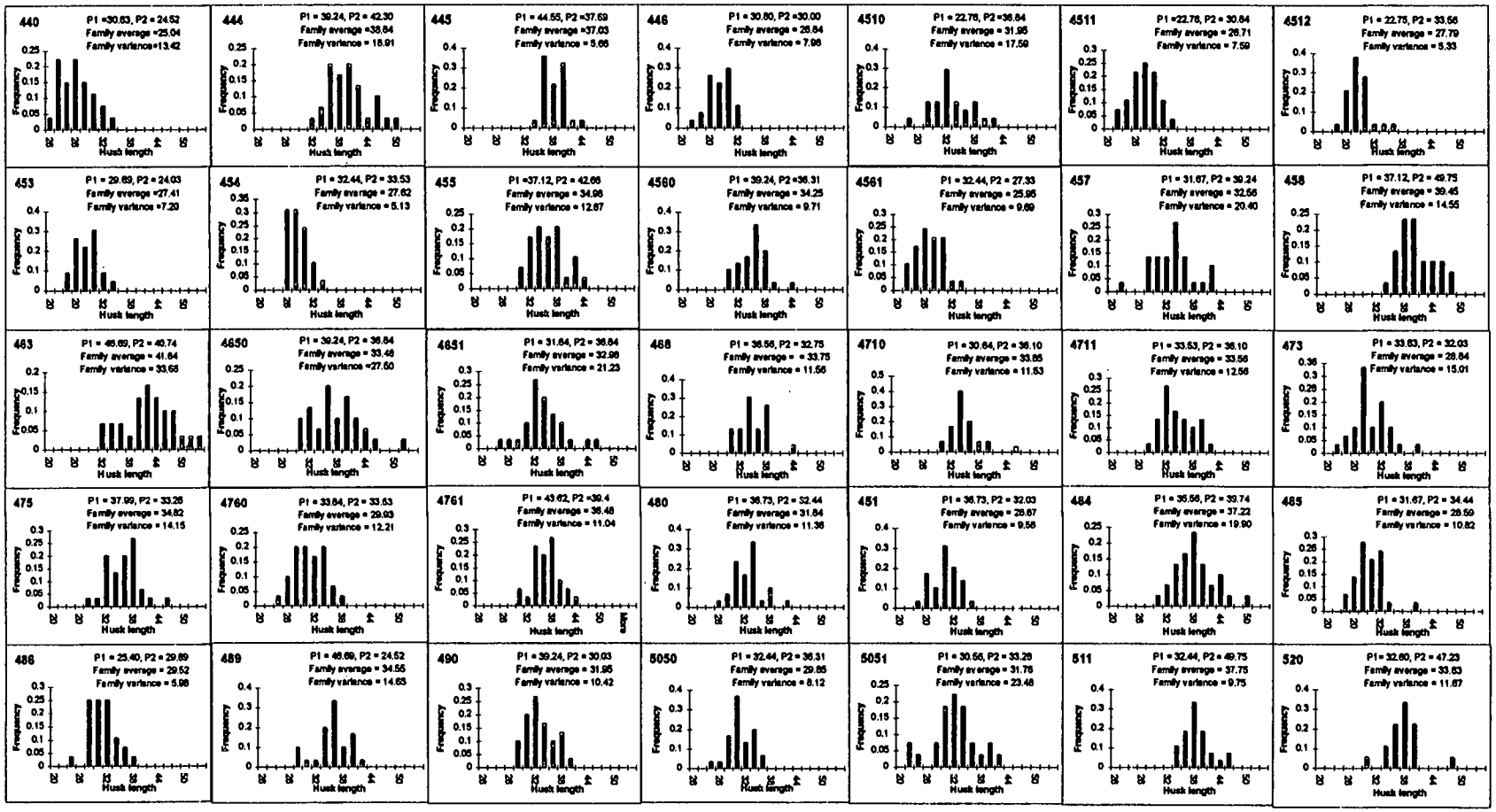

Figure 5.13 Distribution of husk length in the offspring of 35 crosses

Relative husk length

Actually, husk length relative to nut length affects the ability of nuts to fall free of the husks. Therefore, we observed inheritance of relative husk length. There were 14 crosses whose progeny means were smaller than the shorter parent (Fig. 5.14).

Time of leafing out

Time of leafing out is not a very important trait in OSU hazelnut breeding program, as spring frosts are extremely rare in Oregon. In other regions, however, genotypes that leaf out too early are much more subject to spring frost damage. In our population, transgressive segregation for late leafing out was very common. There were 20 crosses whose progeny means were later than the later leafing parent, and only one whose progeny mean was earlier than the earlier leafing parent (Fig. 5.15). It is noted that leafing out varies with age (Thompson et al., 1996). This is probably one reason why seedlings had larger progeny means.

Nut maturity

Nut maturity is an important trait in the OSU hazelnut breeding program. In Oregon, autumn rains begin in October. It is better to complete harvest before the rains begin. If the nut maturity of 'TGDL' is set at 1, that of improved selections and varieties is less than 6 (the rating for 'Barcelona'). Early-maturing seedlings are very common in the OSU hazelnut breeding population. A high frequency of early maturing offspring were observed unless both parents of a cross were very late maturing. Nut maturity in most crosses was around the mid-parent values. The progeny means in 12 crosses were

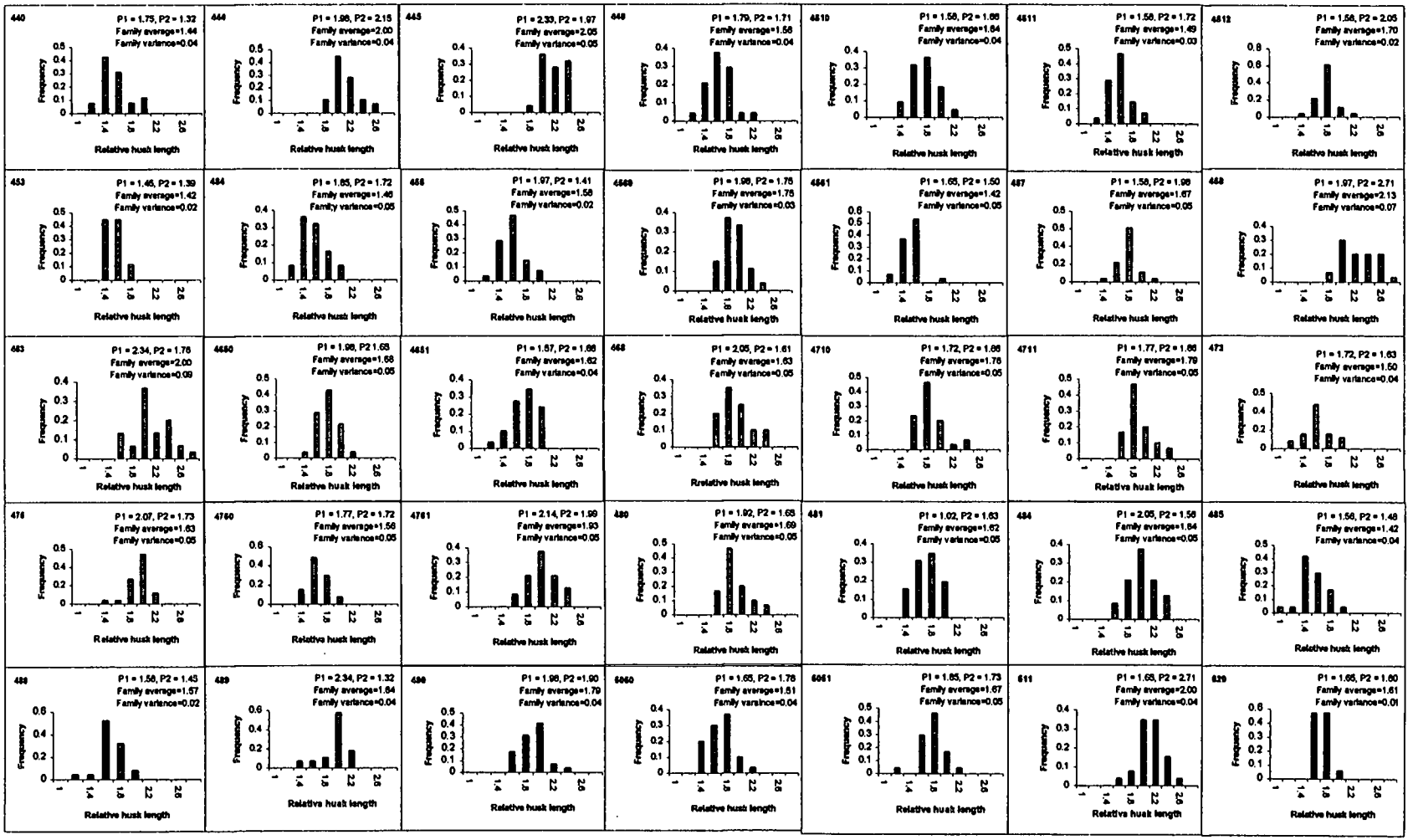

Figure 5.14 Distribution of relative husk length in the offspring of 35 crosses

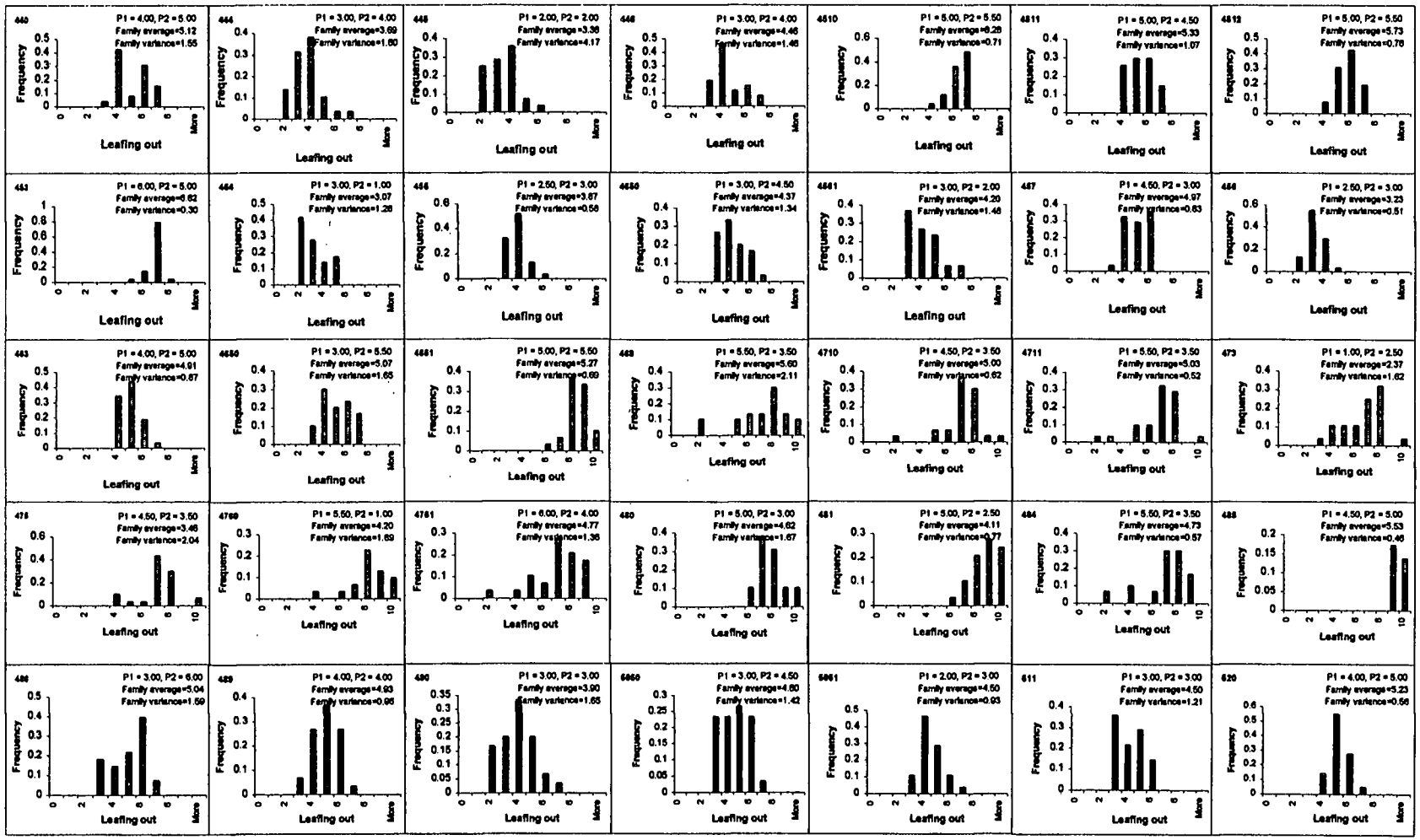

Figure 5.15 Distribution of time of leafing out in the offspring of 35 crosses

earlier than the earlier maturing parent. The progeny means in 3 crosses were later than the later parent (Fig. 5.16).

Time of catkin elongation

Time of catkin elongation is an important consideration in the selection of pollinizers in the OSU hazelnut breeding program. Large variation was observed within crosses and transgressive segregation was common. There were 15 crosses whose progeny means were later than the later parent, and only one cross whose progeny mean was earlier than the earlier parent values (Fig. 5.17). This trait is sensitive to temperature fluctuation after chilling requirements have been satisfied.

Date of opening of female flowers

Date of opening of female flowers is not an important trait in the OSU breeding program either. Similarly, large variation within a cross was observed and transgressive segregation was common. There were 12 crosses whose progeny means were later than the later parent, and 2 crosses whose progeny means were earlier than the earlier parent (Fig. 5.18). Bi-modal distributions were common.

The bi-modal distributions for TCE and DOFF in our study seem to be due to a period of cold weather (January 30, 1996 to February 4, 1996). Both traits are a function of heat unit accumulation after the chilling requirement has been satisfied (Mehlenbacher, 1991b). Warmer temperature after rest stimulates catkin elongation and stigma exsertion from female flowers. Therefore, the distributions of the two traits might also vary greatly from year to year as a function of temperature.

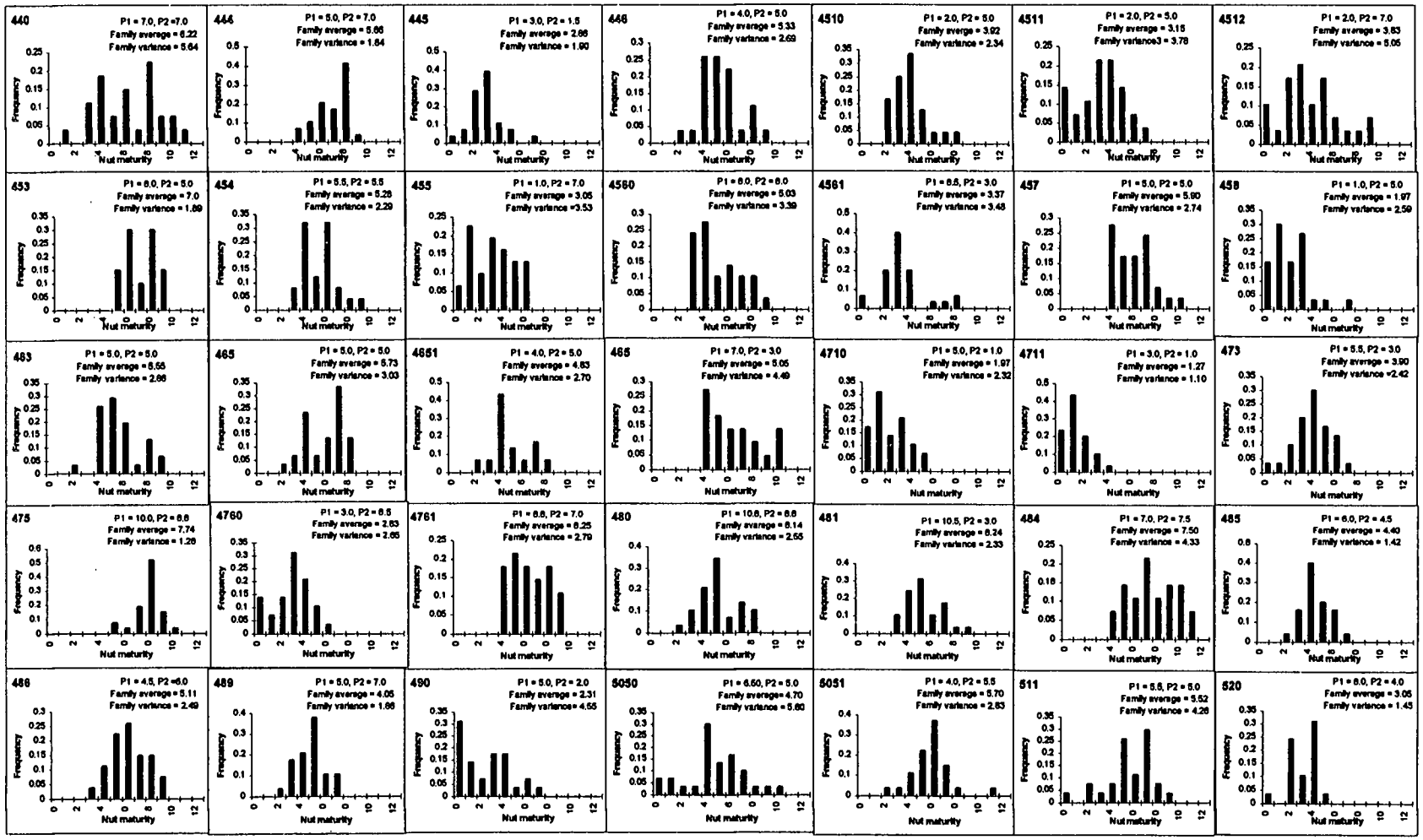

Figure 5.16 Distribution of nut maturity in the offspring of 35 crosses

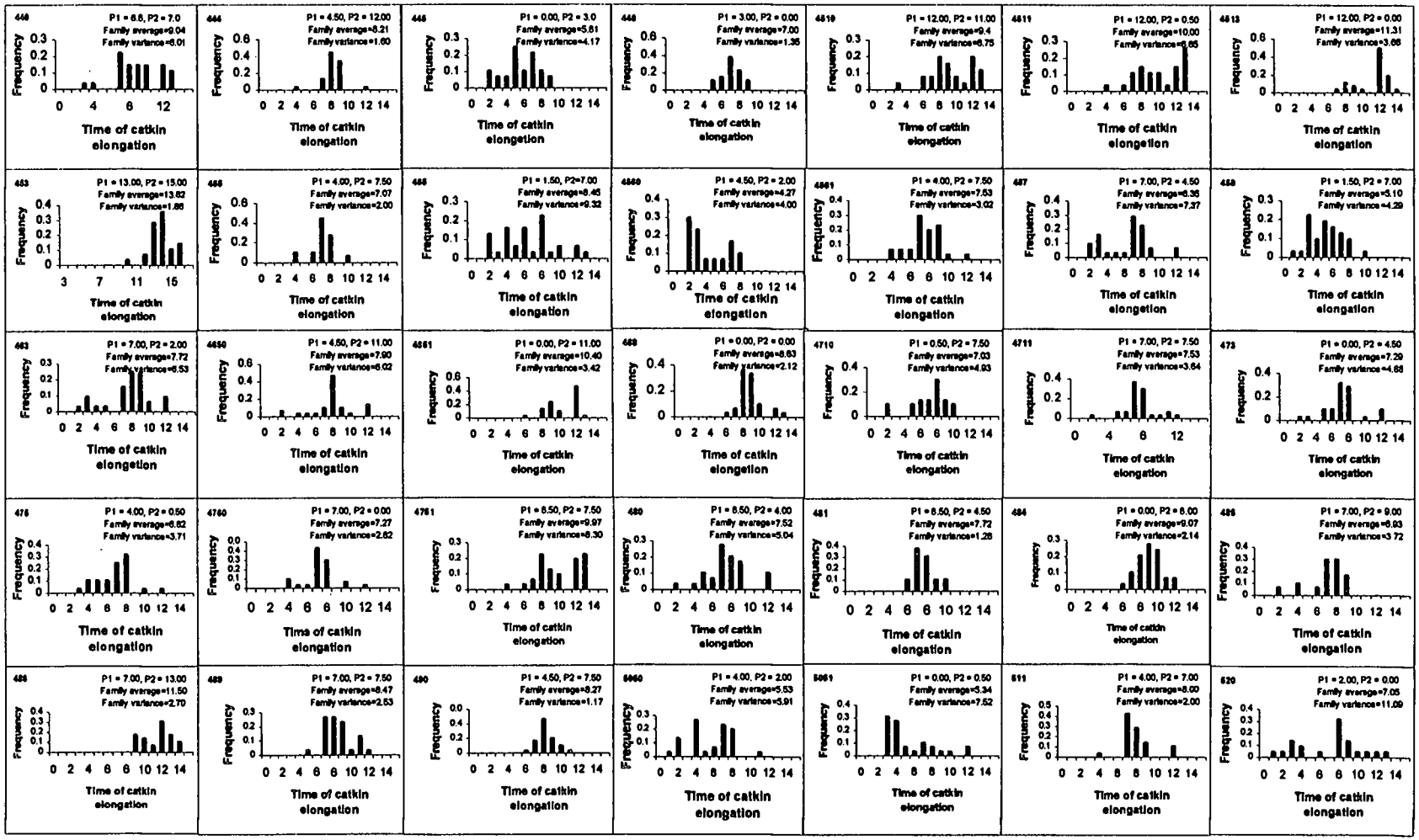

Figure 5.17 Distribution of time of catkin elongation in the offspring of 35 crosses

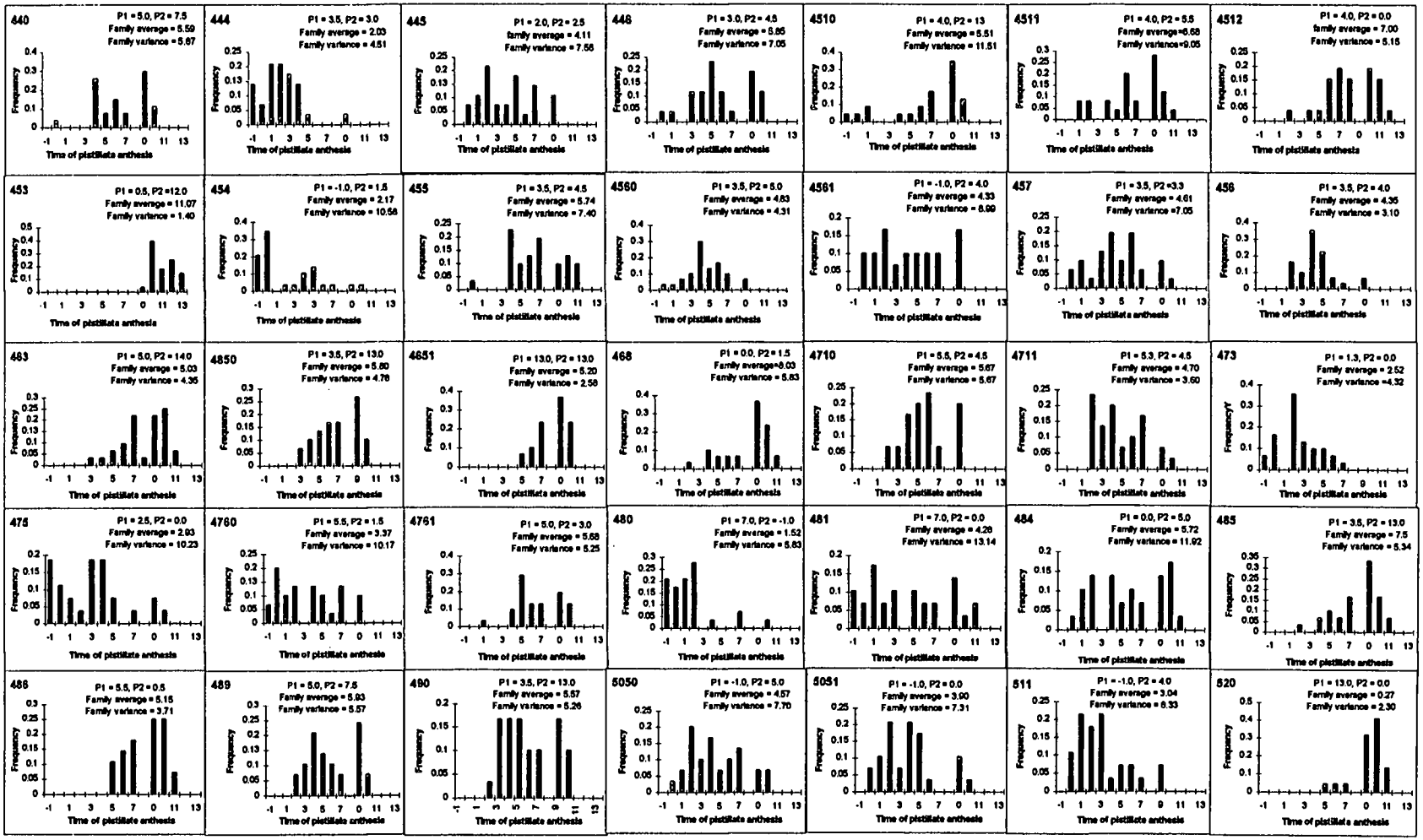

Figure 5.18 Distribution of day of opening of female flowers in the offspring of 35 crosses

Conclusion

All 17 traits exhibited continuous variation in the 35 progenies examined. No bimodal or trimodal distributions indicating Mendelian segregation for major genes were observed. There appear to be no major gene effects in the progenies observed. Transgressive segregation was common and the improvement of target traits should be easy and rapid. For all traits except blanching ability, choice of parent combinations may be based on midparent values. For blanching ability, if a high frequency of easily blanched kernels is desired, both parents should blanch easily.

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CHAPTER 6

CALCULATION OF GENETIC CORRELATION COEFFICIENTS BASED ON OFFSPRING-PARENT RELATIONSHIPS USING A SPREADSHEET

Abstract

Genetic correlation coefficients can be used to compare efficiency of direct and indirect selection, estimate correlated response to selection and set up index selection. Information on quantitative traits in parent and offspring can be used to estimate genetic correlation coefficients for fruit and nut crops. However, existing statistical packages do not allow easy calculation of genetic correlation coefficients. In this paper, we demonstrate the use of a spreadsheet to quickly estimate genetic correlation coefficients using data on parents and progenies in the OSU hazelnut breeding program. This procedure can be extended to n traits and m crosses.

Introduction

Genetic correlation coefficients between traits are an important genetic parameter in a breeding program. They can be used to compare efficiency of direct selection against indirect selection, estimate correlated response to selection and set up index selection (Falconer, 1981).

The formula, $\frac{COV_{x1y2} + COV_{x2y1}}{2 * \sqrt{COV_{xx} COV_{yy}}}$, is used to estimate genetic correlation coefficients between traits based on the offspring-parent relationship (Becker, 1984; Hansche et al., 1966), where X and Y are two traits, COVxy is the 'cross-variance', and COVxx and COVyy are the offspring-parent covariance of each trait separately. The cross-variance is calculated from trait X in the parents and trait Y in the offspring (COV_{x1y2}) or trait Y in the parents and trait X in the offspring (COV_{x2y1}).

There is no direct output of genetic correlation coefficients from existing statistical applications, although some software packages, such as SAS, can be used to calculate a covariance matrix.

In this paper, we show a procedure which uses a spreadsheet in Excel for Windows 95 on IBM platform (PC computer) to calculate genetic correlation coefficients based on the offspring-parent relationship using data from the OSU hazelnut breeding program.

Original data input

The original data set consists of 35 crosses (full-sib families) investigated in 1995 for 4 traits. The data points are entered in columns of either mid-parent values or progeny means. Each row in the data set contains information from a particular cross for all traits, and each column contains information about a particular trait for all crosses.

Because many data points are used to calculate genetic correlation coefficients, it is best to reserve the row above the first data points for column headings. In our example, the first six column headings are cross code, year, and mid-parent values for nut

length (pnl), nut width (pnw), nut depth (pnd), and % kernel (p%k). The next 4 headings are progeny means for nut length (snl), nut width (snw), nut depth (snd), and %K (s%k). These 4 columns of progeny means in the same order are repeated a second time. The cell locations for the headings range from A2 to N2.

In our example, there are 35 rows, one for each of the 35 crosses. All of the data to be used is in the range A3 to N37. The original data input is illustrated in Fig. 6.1.

Calculation of COVxx, COVyy and COVxy

In the same spreadsheet as the original data are input, we will now use built-in functions in the spreadsheet program to calculate covariances. These functions are accessed by clicking on the f_x button on the Excel tool bar.

In our example, we first calculate the parent-offspring covariance for nut length and then the parent-offspring covariance for other traits. We will place the resulting covariance for nut length in cell C41. The methods are as follows:

a). press the f_x button to get the Paste Function --- step 1 of 2;

b). under "Function Category", highlight statistical function and then under "Function Name" highlight covar function;

c). press the 'OK' button to get the Paste Function --- step 2 of 2;

d). in the box next to array 1, put in the cell locations of mid-parent values for nut length. In the box next to array 2, put in the cell locations of progeny means for nut length. In our example, the cell locations of mid-parent value for nut length range from C3 to C37, and the cell locations of progeny means for nut length range from G3 to G37;

e). press the 'OK' button and finish calculation;

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A1 = Original data input

Original data input

cross code	investigation year	pnl	pnw	pnd	p%k	snl	snw	snd	s%k	snl	snw	snd	s%k
440	1995	18.02	18.87	16.70	47.12	17.37	17.88	16.07	49.99	16.62	17.22	15.55	48.67
444	1995	19.74	18.41	16.49	51.69	19.34	18.17	16.76	54.12	19.26	17.99	16.47	53.65
445	1995	19.09	18.10	16.84	47.56	17.99	18.33	16.46	48.70	17.04	16.88	16.37	48.67
446	1995	17.16	18.00	15.39	47.74	17.47	18.07	15.69	48.77	17.77	18.31	15.84	52.59
453	1995	19.01	16.05	13.11	42.55	19.36	15.55	12.99	43.85	19.25	15.31	12.68	44.42
454	1995	19.58	19.29	16.83	48.36	19.00	17.06	14.52	48.98	19.40	16.93	14.64	48.74
455	1995	24.22	19.84	17.85	43.38	22.19	19.04	16.80	45.17	22.88	18.88	16.56	45.52
457	1995	19.94	18.79	17.03	48.11	19.69	18.23	16.56	47.88	19.11	18.26	16.29	47.03
458	1995	18.65	17.22	16.02	48.54	18.61	17.67	16.10	49.02	19.22	18.81	16.69	46.81
463	1995	21.58	21.40	20.10	46.16	20.94	20.32	19.64	44.39	21.14	19.99	19.03	44.61
468	1995	18.88	16.36	14.61	51.02	18.91	16.82	14.32	51.37	18.82	16.87	14.64	51.13
473	1995	19.56	19.68	17.05	47.82	19.27	18.62	15.94	46.07	19.10	17.94	15.39	47.13
475	1995	18.82	18.60	16.45	51.33	18.88	17.98	15.71	50.22	19.20	18.22	16.18	50.60
480	1995	19.40	18.44	16.11	46.69	19.03	17.86	15.63	48.10	18.75	18.25	15.65	45.40
481	1995	19.38	18.83	16.33	46.15	17.75	18.52	16.18	46.00	17.84	18.69	16.35	46.44
484	1995	21.37	19.62	18.20	47.22	20.23	17.87	16.08	49.65	19.15	17.21	15.11	53.65
485	1995	21.63	20.40	19.01	47.78	20.22	18.61	17.26	49.40	19.09	18.59	17.14	50.09
486	1995	18.34	17.26	14.99	49.19	19.02	17.33	15.16	45.81	19.38	17.50	15.36	46.34
489	1995	19.25	18.77	16.95	48.46	18.81	17.66	16.02	50.17	19.24	17.93	16.38	50.29
490	1995	17.82	16.62	15.44	43.12	17.80	16.07	14.89	49.38	17.89	16.46	15.11	50.59
511	1995	19.04	17.00	15.57	48.76	19.06	16.38	14.87	49.62	18.84	15.73	14.07	49.26
520	1995	22.94	19.03	17.31	50.01	22.60	18.33	16.47	47.73	22.24	18.44	16.15	47.73
4510	1995	18.64	16.91	15.19	41.92	19.54	17.35	14.96	40.89	19.27	16.28	13.72	44.48
4511	1995	16.30	16.09	14.06	50.43	18.04	15.50	13.13	52.41	16.96	15.43	13.04	53.72
4512	1995	16.00	14.53	12.58	48.89	16.43	14.80	12.39	50.83	15.52	14.91	12.13	50.11
4560	1995	20.20	18.82	17.02	46.03	19.06	18.16	16.60	47.89	19.11	19.38	17.56	48.70
4561	1995	19.01	17.81	16.16	49.34	18.33	17.09	15.43	50.06	18.03	16.71	15.35	51.47
4650	1995	21.29	19.93	18.66	43.18	21.46	19.37	17.86	44.89	21.64	18.97	17.95	42.93
4651	1995	19.86	19.49	18.37	46.79	20.33	19.71	18.49	47.44	19.47	18.93	17.76	48.42
4710	1995	18.69	19.18	17.81	55.29	19.38	18.49	17.03	56.29	20.71	18.90	16.88	55.00
4711	1995	19.22	18.20	17.35	54.40	18.85	18.52	17.57	55.93	18.39	19.08	18.21	55.70
4760	1995	19.24	19.11	17.56	50.48	19.22	18.46	17.41	51.25	17.58	18.28	17.31	51.04
4761	1995	20.09	18.49	16.62	46.59	18.43	18.04	16.10	47.55	18.20	17.48	15.80	50.34
5050	1995	20.13	18.41	16.18	46.64	18.66	17.27	15.37	46.68	17.81	17.24	15.45	45.21
5051	1995	17.94	18.56	16.74	50.13	19.12	17.65	15.93	46.97	18.38	17.69	16.04	47.08

Calculation of COVxx, COVyy and COVxy

Sheet1 Sheet2 Sheet3 Sheet4 Sheet5

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Figure 6.1 The format for original data input

f). highlight cell C41, drag the function in cell C41 to other cells to the right in the same row until cell F41 to finish calculating parent-offspring covariances for the other traits.

All of these steps are illustrated in Fig. 6.2. These cells from C41 to F41 represent parent-offspring covariances for nut length, nut width, nut depth, and %K. These cells should be labelled with headings.

The cross covariance of mid-parent values for nut length and progeny means for nut width will now be calculated, and the result placed in cell C44. Repeat steps a) to e) listed above. However, the value to put into the box next to array 2 should now be changed to cells H3 to H37. The cross covariances will be placed in cells C44 to F44. These cells contain the cross covariances for mid-parent value for nut length and progeny mean for nut width (C44), mid-parent value for nut width and progeny mean for nut depth (D44), mid-parent value for nut depth and progeny mean for %K (E44), and mid-parent value for %K and progeny mean for nut length (F44).

Next we will calculate the cross covariance of mid-parent values of nut length and progeny mean of nut depth, and place the result in cell C47. Repeat steps a) to e) listed above. However, the values to put into the box next to array 2 should be changed to cell I3 to cell I37 at this time. The cross covariance of mid-parent value for nut width and progeny mean for %K (D47), mid-parent value for nut depth and progeny mean for nut length (E47), and mid-parent value for %K and progeny mean for nut width (F47).

The same principle is applied to calculation of other cross covariances. Considering these calculation steps, there are three features: i) there are 4 rows for

calculation of covariance of parent-offspring or cross covariance for 4 traits between which genetic correlation coefficients will be computed; ii) there are 4 cells in each row

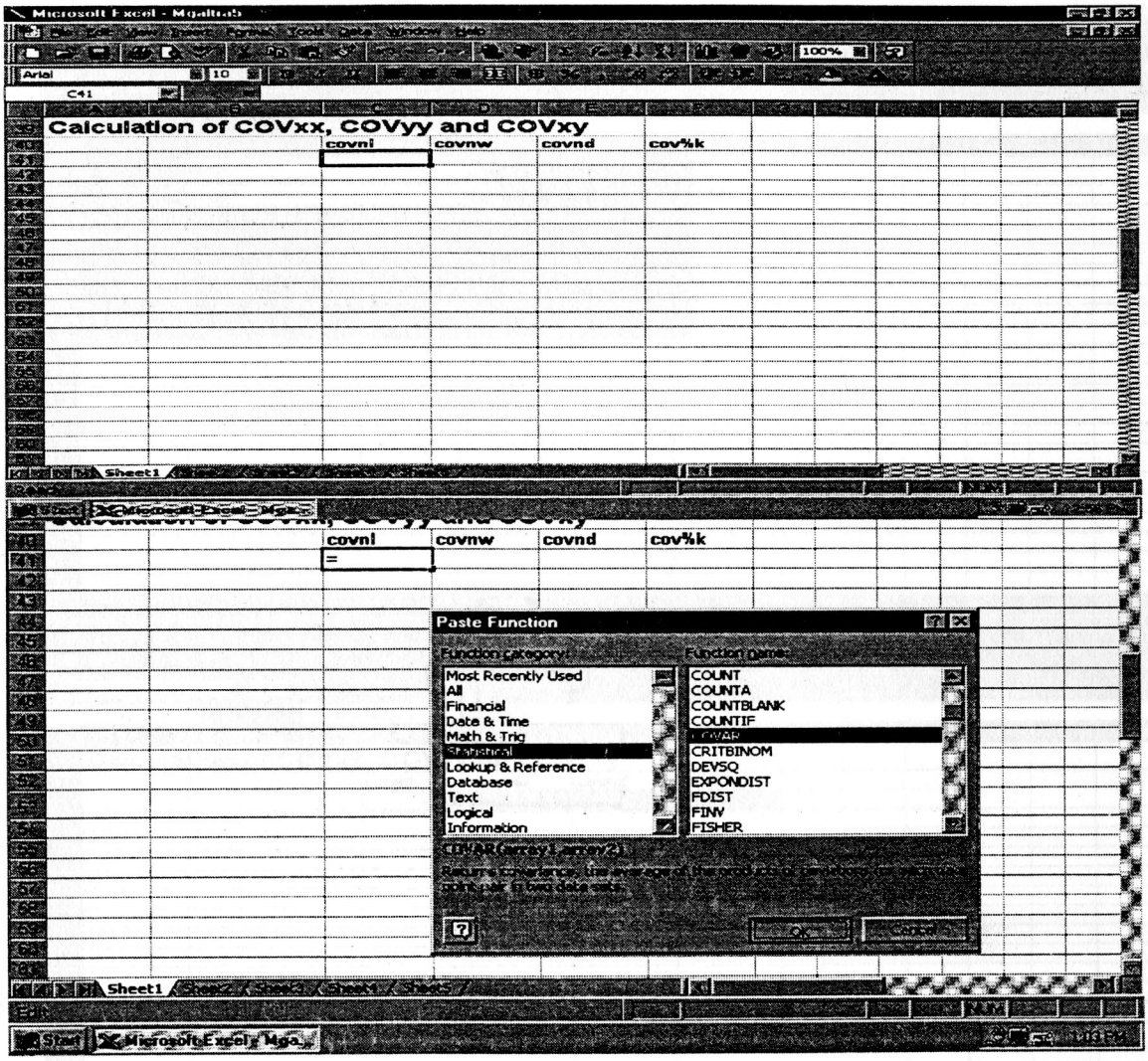

Figure 6.2 The procedure for covariance calculation

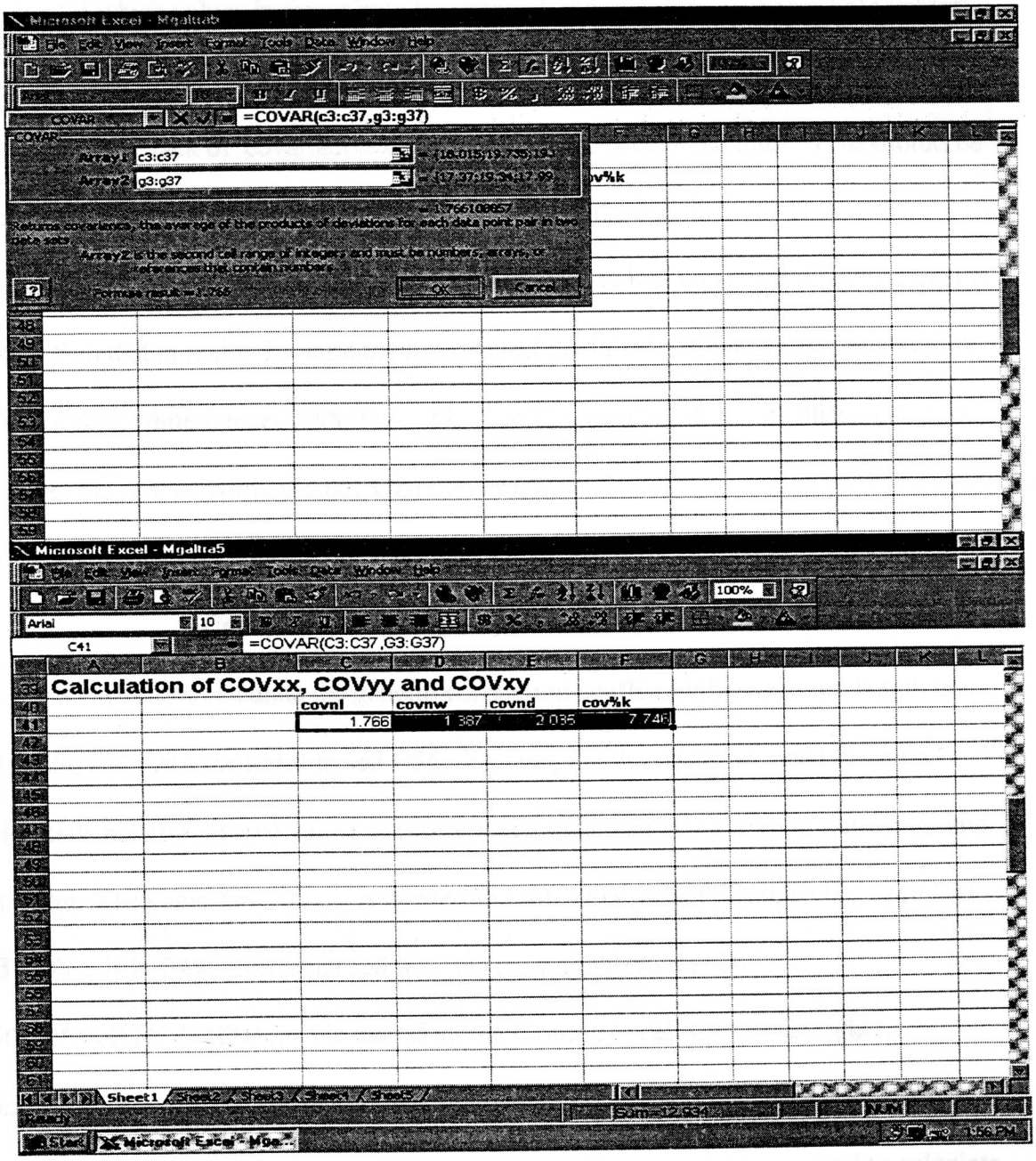

Figure 6.2 The procedure for covariance calculation (con't)

which hold the calculation results of covariance of parent-offspring or cross covariance for 4 traits; iii) the first cell in each row holds the value based on calculation of Paste Function of which values in arrays may be changed, other cells in each row hold values based on calculation by means of dragging the mouse.

To keep track of covariances or cross-covariances between traits, there should be a heading for each cell in each row. The format looks like Fig. 6.3.

It is noticed that values for covariances or cross-covariances calculated in Excel is smaller than that in reality because the spreadsheet uses the formula $COV(X, Y) = (\Sigma XY - \Sigma X\Sigma Y/N)/N$, while Becker (1984) uses $N - 1$ as the denominator. The difference does not affect the genetic correlations, as the denominators cancel.

Calculation of genetic correlation coefficients

We will now calculate the genetic correlation coefficient between nut length and nut width, and place the result in cell C55. To compute the result, we need to know which cells hold the needed values for covariance and cross-covariance of nut length and nut width. The value for COV_{x1y2} is located in C44, COV_{x2y1} is in D50, COV_{xx} is in C41 and COV_{yy} is in D41. So for the cell C55 we input the formula (C44 + D50)/[2*SQRT(C41*D41)]. We then drag the formula in cell C55 to the right to calculate genetic correlation coefficients between nut width and nut depth (D55), and between nut depth and %K (E55). In a new row, similar procedures are used to calculate genetic correlation coefficients between nut length and nut depth, nut width and %K, and

Microsoft Excel - Mgaltra5

A39 = Calculation of COVxx, COVyy and COVxy

	A	B	C	D	E	F
39	Calculation of COVxx, COVyy and COVxy					
40			covnl	covnw	covnd	cov%k
41			1.766	1.387	2.035	7.746
42						
43			covpnlsnw	covpnwsnd	covpnds%k	covp%ksnl
44			1.179	1.669	-0.108	-0.631
45						
46			covpnlsnd	covpnws%k	covpndsnl	covp%ksnw
47			1.377	-0.588	1.220	0.472
48						
49			covpnls%k	covpnwsnl	covpndsnw	covp%ksnd
50			-1.573	1.110	1.467	0.682

Figure 6.3 The format for covariances and cross-covariances among traits

these coefficients are placed in cells C58 to D58. In a new row, a similar method is used to calculate the genetic correlation coefficient between nut length and %K, and the result is placed in C61. The calculation method and format are shown in Fig. 6.4.

Summary Statement

Genetic correlation coefficients based on the offspring-parent relationship can be easily, quickly and precisely calculated in Excel. The procedure can be extended to calculation of genetic correlation coefficients for n traits and m crosses.

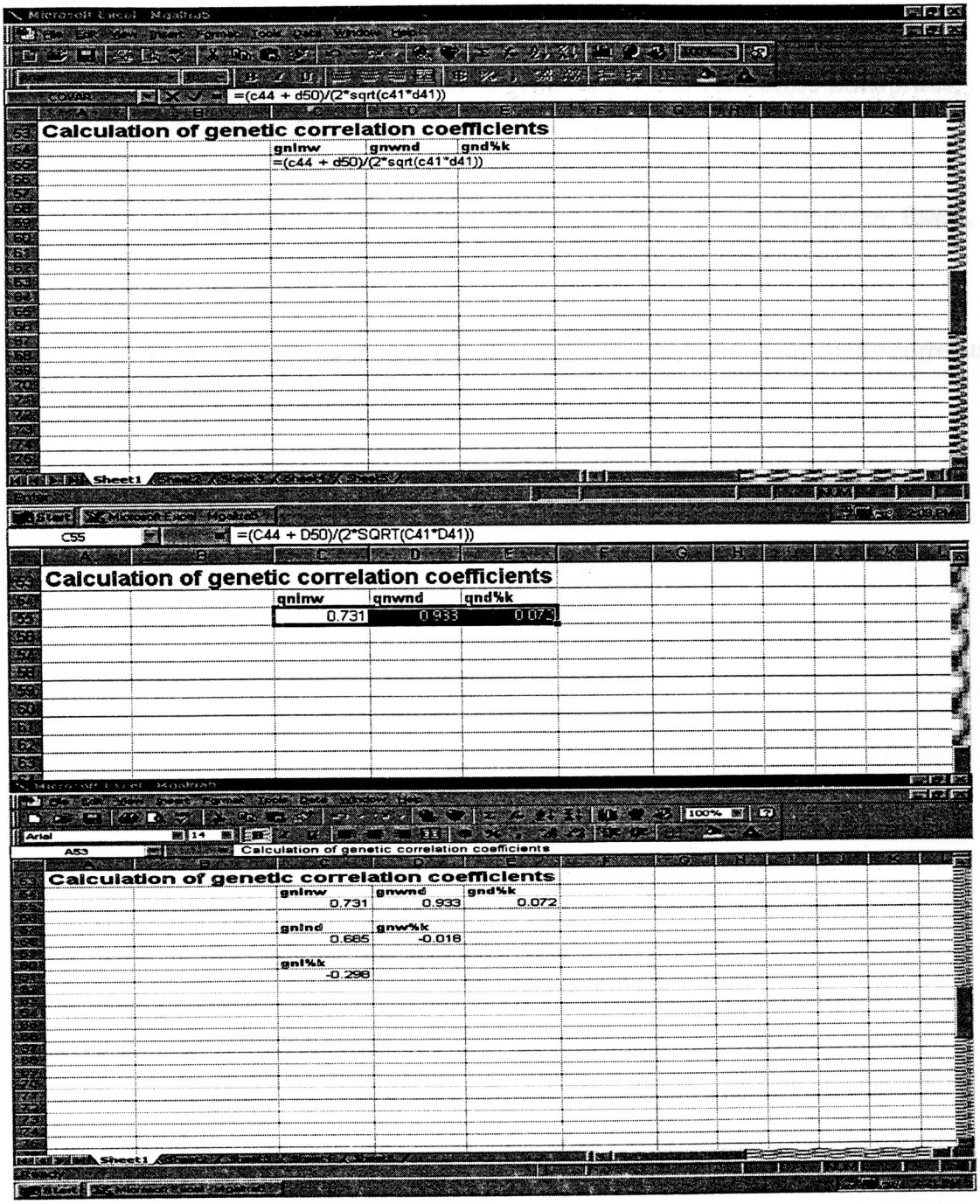

Figure 6.4 The method and format for calculation of genetic correlation coefficients

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CHAPTER 7

SUMMARY

Narrow sense heritability was estimated for 17 hazelnut traits, including 13 nut and kernel traits and 4 phenological traits by regression of offspring means on mid-parent values using data collected over a two-year period. The slopes of the regression lines for the two years were not significantly different for any of the traits. All estimates were high, which suggests that progeny means can be predicted from mid-parent values and response to selection is expected to be rapid for all traits. When progeny means from one year were regressed on mid-parent values from the other year, the estimates were nearly identical with two exceptions. The exceptions are date of opening of female flowers and time of catkin elongation, and the difference in slopes is attributed to temperation variation in the two years.

Analysis of variance components revealed that genotypic variance accounted for most of the phenotypic variance for all traits. Broad sense heritability was very high for all traits, ranging from 0.82 for nut maturity to 0.99 for nut length. The largest genotype x year interaction component was observed for fiber amount, number of nuts per cluster, nut maturity, and date of opening of female flowers, and the broad sense heritability estimates had correspondingly wider confidence intervals. Even for these traits, the genotype x year component was less than 15% of that for genotypes.

Genetic and phenotypic correlation coefficients showed that nut size measurements were highly correlated with each other, as were three phenological traits

(time of catkin elongation, date of opening of female flowers, and time of leafing out). These correlations among nut size measures and among phenological traits may be due, at least in part, to pleiotropy. Interesting correlations were noted between blanching ability and phenological traits; good blanching genotypes tended to be early leafing, have early females, and shed pollen early. These good blanching types also tended to have husks much longer than their nuts. This combination of traits is present in many of the Turkish parents used in the program. The genetic correlation coefficients are also high, but simple correlation coefficients are much lower. The low simple correlation coefficients correspond to a wide scattering of points from individual seedlings, indicating that a few seedlings can be found with the desired level of any two traits. The genetic correlation may be due to linkage disequilibrium. If that is the case, the traits will behave independently in future generations. The three most important traits (% kernel, blanching ability, and nut maturity) were not significantly correlated, and truncation selection could be used to improve all three traits simultaneously.

Not all of the 17 traits are of equal importance in the breeding program. Nut size measurements allow quantification of nut shape through the calculation of shape and compression indexes. A range of nut sizes is acceptable, but round shape is required. In practice, a breeder can determine if shape is sufficiently round or of an acceptable size by visual inspection. High percent kernel (i.e. thin shells) is also highly desirable, and this trait is quantified by weighing kernels and whole nuts and calculating the ratio. Since nuts must be weighed to determine percent kernel, nut weight data would be the preferred measure of nut size.

Easy blanching is also a high priority objective. The broad sense heritability of this trait was 0.95 and narrow sense heritability was 0.64. When poor blanchers (ratings of 6 or 7) are crossed with good blanchers (ratings of 1 or 2), many seedlings will blanch better than the poor parent, but almost none will blanch well (e.g. progeny 489='23.017' x 'VR 20-11'). To obtain a high percentage of seedlings with ratings of 1 or 2, both parents should blanch well. Even then, many seedlings do not blanch well and many combinations are disappointing (e.g. progeny 454 = 'Negret' x 'Tonda di Giffoni'). Unfortunately, the number of really good blanching selections is very small at this time, and very few were found in the whole seedling population in this study.

Free-husking is an essential trait for a variety suited to mechanical harvest. Several factors can prevent nuts from falling free of the husk even when their basal scars turn brown, indicating that they are mature. Long husks (relative to nut length) make it more difficult for the nuts to fall free, and husks constricted beyond the nut prevent the nuts from falling. Clusters of Turkish genotypes often fall with the nuts enclosed in the husk. Even if not constricted, a long tubular husk that tightens as it dries will prevent the nuts from falling free. The presence of a slit on the side of the husk, which allows the husk to open as it dries, allows many nuts to fall free. Nuts can also adhere to the husk in different ways. The nuts may adhere to the husk at the basal scar ("nuts glued in the husk") as do blanks in most varieties. The nuts may adhere to the husk at the edge of the basal scar. And in a few genotypes some nuts are fused to the husk. The free-husking trait is complex because any one of these many factors can prevent the nuts from falling free at maturity.

Nut maturity is also an important trait, and early maturity is highly desirable. The number of very early maturing genotypes available for use as parents in breeding is very limited, and very early maturing seedlings were rare in our population. The histograms of individual progenies show that transgressive segregation for early maturity is common. As mentioned above, many things can prevent mature nuts from falling to the ground. By carefully choosing parent combinations, one should be able to obtain early maturing seedlings from many different sources.

Existing statistical packages do not allow easy calculation of genetic correlation coefficients for tree fruit and nut crops. The use of a spreadsheet to quickly estimate genetic correlation coefficients is demonstrated.

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APPENDIX

Table A1 Genotype means in different years for nut width

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Fusco Rubra	14.33	Fusco Rubra	12.68	Fusco Rubra	14.55
026.072	15.22	026.072	14.52	026.072	14.96
Contorta	15.57	Contorta	15.68	Contorta	14.96
Aurea	15.81	054.039	16.11	Aurea	15.68
Casina	17.60	VR17-15	16.26	Mortarella	17.55
054.039	17.92	Mortarella	16.33	Casina	17.88
Mortarella	18.21	Aurea	16.37	054.039	18.28
054.021	18.70	Casina	16.38	VR17-15	18.62
VR17-15	18.79	055.077	17.05	Ribet	18.70
Sant Jaume	18.81	255.003	17.54	166.034	18.83
179.043	18.87	225.077	17.73	Daviana	18.93
225.077	19.05	GH140-4	17.79	Negret	19.06
Ribet	19.06	166.034	17.84	162.017	19.13
Negret	19.21	162.017	17.87	255.003	19.17
166.034	19.26	Negret	17.89	VR20-11	19.19
055.077	19.26	054.021	18.11	055.077	19.31
VR20-11	19.27	244.001	18.14	Segorbe	19.45
162.017	19.44	TGDL	18.33	GH140-4	19.53
244.001	19.59	179.043	18.67	179.043	19.54
255.003	19.72	Willamette	18.71	183.060	19.55
Daviana	19.81	VR20-11	18.77	054.021	19.64
TGDL	19.88	023.017	18.77	225.077	19.76
233.007	20.01	183.060	18.79	244.001	19.87
GH140-4	20.10	233.007	18.81	Willamette	19.96
Willamette	20.20	246.128	18.84	TGDL	19.98
246.128	20.54	Tonda di Giffoni	18.84	RG1	20.15
055.129	20.65	055.129	18.85	055.129	20.22
RG1	20.85	Ribet	18.86	Sant Jaume	20.25
023.017	20.87	Segorbe	18.93	246.128	20.30
Segorbe	20.88	245.094	18.99	233.007	20.37
183.060	21.21	Sant Jaume	19.15	Gem	20.73
Tonda di Giffoni	21.34	Daviana	19.25	Tonda di Giffoni	20.80
245.094	21.51	Birk5-6	19.33	Birk5-6	21.06
Birk5-6	21.61	RG1	19.50	023.017	21.23
Tonda Romana	22.09	186.080	20.23	245.094	21.30
Hall's Giant	22.60	Tonda Romana	20.68	Hall's Giant	21.36
186.080	22.99	Gem	21.35	Tonda Romana	21.45
Gem	23.11	Hall's Giant	21.70	039.044	21.68
Brixnut	23.46	039.044	21.94	Brixnut	22.22
039.044	24.17	Brixnut	22.86	186.080	22.57
GH88-14	24.69	GH88-14	24.02	GH88-14	24.24

Table A2 Genotype means in different years for nut depth

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Fusco Rubra	11.66	Fusco Rubra	10.24	Contorta	12.18
Contorta	12.72	Contorta	12.88	Fusco Rubra	12.20
Aurea	13.07	Aurea	13.31	Aurea	12.93
026.072	14.02	026.072	13.70	026.072	13.74
Mortarella	15.49	VR17-15	14.10	Mortarella	14.78
VR17-15	15.86	Mortarella	14.29	VR17-15	15.06
054.021	15.92	Casina	14.93	Negret	15.52
179.043	15.98	Negret	15.50	Casina	15.85
Negret	16.15	054.039	15.63	179.043	16.18
Casina	16.26	054.021	15.80	VR20-11	16.59
VR20-11	16.81	179.043	15.95	Segorbe	16.95
TGDL	16.96	162.017	16.01	054.039	16.95
Sant Jaume	17.14	244.001	16.39	Daviana	16.97
Ribet	17.21	055.077	16.40	Ribet	17.07
054.039	17.22	TGDL	16.41	162.017	17.18
166.034	17.36	166.034	16.59	054.021	17.24
244.001	17.39	GH140-4	16.60	244.001	17.33
162.017	17.50	VR20-11	16.64	TGDL	17.36
233.007	17.78	245.094	16.71	166.034	17.52
055.077	17.90	183.060	16.75	Birk5-6	17.63
Segorbe	17.94	225.077	16.82	183.060	17.73
Daviana	18.00	Segorbe	16.85	233.007	17.77
Willamette	18.16	Tonda di Giffoni	16.85	GH140-4	17.90
245.094	18.19	Ribet	16.88	255.003	17.94
GH140-4	18.23	Birk5-6	16.88	Willamette	17.95
Birk5-6	18.35	255.003	16.96	055.077	17.98
225.077	18.51	233.007	16.97	RG1	18.08
RG1	18.56	246.128	17.09	Sant Jaume	18.20
255.003	18.62	186.080	17.11	Gem	18.23
246.128	18.65	Willamette	17.18	246.128	18.38
023.017	18.91	023.017	17.26	Tonda di Giffoni	18.52
183.060	19.05	Sant Jaume	17.28	225.077	18.61
186.080	19.19	Daviana	17.64	245.094	18.70
Tonda di Giffoni	19.20	055.129	17.73	055.129	18.90
055.129	19.32	RG1	17.89	186.080	18.93
Tonda Romana	19.54	Tonda Romana	18.15	Tonda Romana	18.98
Gem	20.48	Gem	19.29	023.017	19.13
Brixnut	20.85	Hall's Giant	20.90	Brixnut	20.33
Hall's Giant	21.20	039.044	21.13	Hall's Giant	20.71
039.044	22.93	Brixnut	21.46	039.044	21.07
GH88-14	23.70	GH88-14	22.94	GH88-14	22.75

Table A3 Genotype means in different years for nut shape index

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Contorta	0.66	Gem	0.69	Contorta	0.65
Gem	0.71	Contorta	0.69	Gem	0.67
Daviana	0.75	Daviana	0.70	Daviana	0.68
Aurea	0.83	Mortarella	0.75	Mortarella	0.80
Mortarella	0.83	Fusco Rubra	0.78	Negret	0.83
054.021	0.85	244.001	0.85	Aurea	0.83
Fusco Rubra	0.87	Negret	0.85	Brixnut	0.87
Negret	0.87	Aurea	0.86	VR17-15	0.88
Ribet	0.88	054.021	0.87	Segorbe	0.89
179.043	0.89	054.039	0.87	Ribet	0.89
Willamette	0.91	VR17-15	0.87	Fusco Rubra	0.89
Brixnut	0.91	Segorbe	0.87	026.072	0.89
244.001	0.91	Brixnut	0.88	179.043	0.90
233.007	0.91	055.077	0.88	244.001	0.90
Hall's Giant	0.91	179.043	0.88	Casina	0.90
026.072	0.92	Ribet	0.89	Hall's Giant	0.90
Segorbe	0.93	026.072	0.89	Willamette	0.92
054.039	0.94	Casina	0.90	255.003	0.92
VR17-15	0.94	Tonda di Giffoni	0.91	054.021	0.94
Sant Jaume	0.95	023.017	0.91	VR20-11	0.94
TGDL	0.95	Willamette	0.91	039.044	0.94
VR20-11	0.96	255.003	0.91	233.007	0.94
055.077	0.96	233.007	0.91	054.039	0.95
Casina	0.96	Hall's Giant	0.91	162.017	0.95
023.017	0.97	TGDL	0.92	Birk5-6	0.95
225.077	0.97	162.017	0.92	Tonda di Giffoni	0.96
Tonda di Giffoni	0.98	039.044	0.93	023.017	0.97
255.003	0.99	245.094	0.94	055.077	0.97
162.017	0.99	Birk5-6	0.94	225.077	0.97
245.094	1.01	055.129	0.94	Sant Jaume	0.99
039.044	1.01	225.077	0.94	TGDL	0.99
Tonda Romana	1.02	VR20-11	0.96	245.094	0.99
GH88-14	1.04	Sant Jaume	0.96	GH88-14	1.00
RG1	1.04	Tonda Romana	1.00	Tonda Romana	1.01
Birk5-6	1.04	GH88-14	1.01	RG1	1.01
055.129	1.04	166.034	1.02	166.034	1.03
166.034	1.06	183.060	1.02	055.129	1.03
183.060	1.12	GH140-4	1.03	183.060	1.05
GH140-4	1.12	RG1	1.04	GH140-4	1.07
186.080	1.17	186.080	1.09	186.080	1.13
246.128	1.27	246.128	1.12	246.128	1.21

Table A4 Genotype means in different years for nut compression index

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
225.077	1.03	054.039	1.03	039.044	1.03
054.039	1.04	255.003	1.04	Hall's Giant	1.03
GH88-14	1.04	Hall's Giant	1.04	225.077	1.06
039.044	1.06	039.044	1.04	GH88-14	1.07
255.003	1.06	055.077	1.04	055.129	1.07
Hall's Giant	1.07	GH88-14	1.05	255.003	1.07
055.129	1.07	225.077	1.06	055.077	1.07
055.077	1.08	026.072	1.06	166.034	1.08
Casina	1.08	055.129	1.06	054.039	1.08
026.072	1.09	Brixnut	1.07	026.072	1.09
Sant Jaume	1.10	GH140-4	1.07	GH140-4	1.09
246.128	1.10	166.034	1.08	Brixnut	1.10
Daviana	1.10	023.017	1.09	Ribet	1.10
023.017	1.10	Willamette	1.09	183.060	1.10
GH140-4	1.10	RG1	1.09	246.128	1.11
Ribet	1.11	Daviana	1.09	023.017	1.11
166.034	1.11	Casina	1.10	Sant Jaume	1.11
162.017	1.11	246.128	1.10	Willamette	1.11
Tonda di Giffoni	1.11	244.001	1.11	162.017	1.11
Willamette	1.11	233.007	1.11	Daviana	1.12
183.060	1.11	Sant Jaume	1.11	RG1	1.12
RG1	1.12	Gem	1.11	Tonda di Giffoni	1.12
233.007	1.13	162.017	1.12	Casina	1.13
Brixnut	1.13	TGDL	1.12	Tonda Romana	1.13
244.001	1.13	Ribet	1.12	054.021	1.14
Tonda Romana	1.13	Tonda di Giffoni	1.12	Gem	1.14
Gem	1.13	183.060	1.12	245.094	1.14
VR20-11	1.15	Segorbe	1.13	233.007	1.15
Segorbe	1.17	VR20-11	1.13	244.001	1.15
TGDL	1.17	245.094	1.14	Segorbe	1.15
054.021	1.18	Tonda Romana	1.14	TGDL	1.15
Mortarella	1.18	Mortarella	1.14	VR20-11	1.16
Birk5-6	1.18	054.021	1.15	Mortarella	1.19
179.043	1.18	Birk5-6	1.15	186.080	1.19
245.094	1.18	VR17-15	1.16	Birk5-6	1.20
VR17-15	1.19	Negret	1.16	179.043	1.21
Negret	1.19	179.043	1.17	Aurea	1.21
186.080	1.20	186.080	1.18	Contorta	1.23
Aurea	1.21	Contorta	1.22	VR17-15	1.24
Contorta	1.23	Aurea	1.23	Negret	1.25
Fusco Rubra	1.23	Fusco Rubra	1.24	Fusco Rubra	1.32

Table A5 Genotype means in different years for nut weight

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Fusco Rubra	11.55	Fusco Rubra	9.36	Fusco Rubra	13.80
026.072	17.95	225.077	17.13	026.072	18.16
Aurea	19.21	026.072	17.52	Aurea	19.38
Casina	20.30	Casina	19.94	Contorta	19.95
Contorta	20.38	054.039	20.22	166.034	22.01
Mortarella	21.23	183.060	20.37	054.039	22.89
166.034	23.20	054.021	20.43	Mortarella	23.30
054.021	23.27	VR17-15	20.69	Casina	23.54
054.039	24.17	Aurea	20.78	Ribet	25.06
VR17-15	24.41	Contorta	21.40	VR17-15	25.16
246.128	25.15	GH140-4	21.41	GH140-4	25.56
VR20-11	25.62	Mortarella	21.88	246.128	25.75
Ribet	25.81	166.034	21.94	183.060	25.82
GH88-14	25.99	055.077	22.03	055.129	25.89
Negret	26.04	246.128	22.29	054.021	25.90
RG1	26.27	255.003	22.71	RG1	26.02
179.043	26.31	162.017	22.81	255.003	26.20
225.077	26.51	RG1	23.38	055.077	26.34
Sant Jaume	26.62	186.080	23.54	VR20-11	26.95
255.003	27.33	Negret	24.04	179.043	27.32
055.077	27.79	245.094	24.34	Negret	27.55
183.060	27.94	244.001	24.59	162.017	27.84
244.001	28.00	VR20-11	25.01	225.077	28.36
TGDL	28.87	055.129	25.48	TGDL	28.66
233.007	28.88	Sant Jaume	25.52	186.080	29.30
055.129	29.27	TGDL	25.74	244.001	30.56
162.017	29.49	023.017	25.76	Segorbe	30.65
023.017	31.06	Tonda Romana	25.93	Sant Jaume	30.77
Birk5-6	31.35	Birk5-6	26.19	Birk5-6	31.42
Daviana	32.01	Willamette	26.53	Daviana	31.56
186.080	32.51	Ribet	26.68	Tonda di Giffoni	32.42
Tonda di Giffoni	32.59	233.007	26.76	233.007	32.43
Willamette	33.20	179.043	27.46	Tonda Romana	33.15
Segorbe	33.44	Segorbe	29.25	Willamette	34.12
245.094	33.71	Tonda di Giffoni	31.17	245.094	34.15
GH140-4	34.33	Daviana	32.77	023.017	35.34
Tonda Romana	36.18	039.044	38.16	Brixnut	36.49
039.044	42.06	Hall's Giant	39.20	039.044	36.89
Brixnut	43.80	Brixnut	42.56	Hall's Giant	40.52
Hall's Giant	44.50	GH88-14	46.53	Gem	45.42
Gem	55.68	Gem	53.44	GH88-14	46.44

Table A6 Genotype means in different years for kernel weight

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Fusco Rubra	5.34	Fusco Rubra	4.26	Fusco Rubra	6.53
026.072	6.97	026.072	6.69	026.072	7.14
Aurea	7.77	Aurea	7.84	Aurea	7.66
Contorta	9.90	225.077	8.46	Contorta	9.39
Casina	11.08	183.060	8.98	054.039	10.98
VR17-15	11.32	VR17-15	9.56	VR17-15	11.48
054.039	11.43	054.039	9.75	GH140-4	12.15
Sant Jaume	11.44	GH140-4	10.08	Mortarella	12.43
Mortarella	11.62	Contorta	10.14	183.060	12.46
GH88-14	12.03	Casina	10.42	166.034	12.61
179.043	12.27	245.094	10.74	Ribet	12.61
054.021	12.56	244.001	10.78	Casina	12.87
246.128	12.59	Mortarella	10.91	246.128	13.01
TGDL	12.83	055.077	11.15	TGDL	13.22
244.001	12.98	054.021	11.31	179.043	13.25
166.034	13.01	162.017	11.32	Sant Jaume	13.48
VR20-11	13.08	Sant Jaume	11.36	055.077	13.56
Negret	13.15	246.128	11.36	Segorbe	13.78
RG1	13.18	186.080	11.60	VR20-11	13.78
183.060	13.19	Negret	11.85	Negret	13.81
Ribet	13.84	023.017	12.03	162.017	13.98
225.077	13.97	166.034	12.13	244.001	14.13
055.077	14.05	255.003	12.16	054.021	14.48
233.007	14.23	VR20-11	12.55	RG1	14.60
Segorbe	14.70	TGDL	12.57	055.129	14.60
Tonda di Giffoni	14.91	Willamette	12.76	255.003	14.75
255.003	14.91	Tonda Romana	12.81	225.077	14.84
162.017	15.02	Ribet	12.84	186.080	14.86
023.017	15.17	Segorbe	12.86	Tonda di Giffoni	15.49
245.094	15.45	RG1	12.93	245.094	15.69
055.129	15.59	233.007	13.12	233.007	15.74
GH140-4	15.63	179.043	13.23	Brixnut	15.82
186.080	15.72	Birk5-6	13.89	Hall's Giant	16.29
Tonda Romana	16.28	055.129	14.07	Daviana	16.66
Willamette	16.43	Tonda di Giffoni	14.79	Willamette	16.75
Birk5-6	16.87	Hall's Giant	14.91	Tonda Romana	16.90
Daviana	17.01	Daviana	16.71	Birk5-6	17.09
Hall's Giant	17.89	Brixnut	17.96	023.017	17.55
Brixnut	18.66	039.044	18.09	Gem	19.18
039.044	20.97	Gem	20.24	039.044	19.57
Gem	21.14	GH88-14	20.59	GH88-14	20.57

Table A7 Genotype means in different years for fiber amount

1994		1995		1996	
GENOTYPE	LSMEAN	GENOTYPE	LSMEAN	GENOTYPE	LSMEAN
023.017	1	023.017	1	023.017	1
055.077	1	055.077	1	166.034	1
166.034	1	166.034	1	233.007	1
179.043	1	225.077	1	Contorta	1
233.007	1	233.007	1	GH140-4	1
Contorta	1	245.094	1	Ribet	1
Ribet	1	246.128	1	179.043	1.5
Sant Jaume	1.25	Contorta	1	255.003	1.5
245.094	1.5	Fusco Rubra	1	Tonda di Giffoni	1.75
054.021	2	GH140-4	1	054.021	2
225.077	2	Ribet	1	055.077	2
246.128	2	255.003	1.5	055.129	2
255.003	2	Birk5-6	1.75	245.094	2
Daviana	2	039.044	2	246.128	2
Gem	2	054.021	2	Brixnut	2
GH88-14	2	054.039	2	Daviana	2
Mortarella	2	179.043	2	Gem	2
Segorbe	2	183.060	2	Mortarella	2
Tonda di Giffoni	2	186.080	2	Sant Jaume	2
Birk5-6	2.5	Daviana	2	Tonda Romana	2
Brixnut	2.5	Gem	2	186.080	2.5
Fusco Rubra	2.5	Hall's Giant	2	244.001	2.5
GH140-4	2.5	Mortarella	2	Birk5-6	2.5
RG1	2.5	Sant Jaume	2	Hall's Giant	2.5
VR20-11	2.5	Segorbe	2	Negret	2.5
039.044	3	Tonda di Giffoni	2	Segorbe	2.5
054.039	3	VR20-11	2	VR20-11	2.5
055.129	3	Willamette	2	Willamette	2.5
162.017	3	244.001	2.25	RG1	2.75
183.060	3	055.129	2.5	026.072	3
186.080	3	Brixnut	2.5	039.044	3
244.001	3	Negret	2.5	054.039	3
Casina	3	RG1	2.5	162.017	3
Hall's Giant	3	Tonda Romana	2.5	183.060	3
Negret	3	026.072	3	225.077	3
Tonda Romana	3	162.017	3	Casina	3
Willamette	3	Aurea	3	Fusco Rubra	3
VR17-15	3.5	Casina	3	GH88-14	3
026.072	4	GH88-14	3	VR17-15	3
Aurea	4	TGDL	3	Aurea	4
TGDL	4	VR17-15	3	TGDL	4

Table A8 Genotype means in different years for blanching ability

1994		1995		1996	
GENOTYPE	LSMEAN	GENOTYPE	LSMEAN	GENOTYPE	LSMEAN
026.072	1	026.072	1	Negret	1
225.077	1	054.039	1	225.077	1.25
Mortarella	1	Mortarella	1	244.001	1.25
Tonda di Giffoni	1	Negret	1	Birk5-6	1.5
244.001	1.25	023.017	1.25	023.017	1.75
Negret	1.25	186.080	1.25	026.072	2
023.017	1.5	Tonda di Giffoni	1.5	054.039	2
055.077	1.5	GH140-4	1.75	Tonda di Giffoni	2
055.129	1.5	055.129	2	162.017	2.25
245.094	1.5	244.001	2	186.080	2.25
Birk5-6	1.5	Birk5-6	2	Hall's Giant	2.5
TGDL	1.5	TGDL	2.75	TGDL	2.5
186.080	1.75	225.077	3	Willamette	2.5
GH140-4	1.75	Aurea	3	245.094	2.75
054.039	2	Contorta	3	Mortarella	2.75
255.003	2.25	Hall's Giant	3	055.077	3
162.017	2.5	162.017	3.25	055.129	3
Sant Jaume	2.5	245.094	3.25	Gem	3
Willamette	2.75	Willamette	3.25	183.060	3.5
179.043	3	055.077	3.5	Aurea	3.5
183.060	3	179.043	3.5	Contorta	3.5
Aurea	3	255.003	3.5	166.034	3.75
Hall's Giant	3	Segorbe	3.75	255.003	4
Segorbe	3	054.021	4	Ribet	4
Brixnut	3.75	183.060	4	Sant Jaume	4
Ribet	3.75	RG1	4	179.043	4.25
054.021	4	Ribet	4	Segorbe	4.25
Contorta	4	Sant Jaume	4	RG1	4.75
Daviana	4	039.044	4.25	039.044	5
GH88-14	4	246.128	4.25	054.021	5
Casina	4.25	166.034	4.5	Daviana	5
039.044	5	Brixnut	5	GH140-4	5
166.034	5	Casina	5	Brixnut	5.5
RG1	5	Daviana	5	233.007	6
VR17-15	5	GH88-14	5	246.128	6
VR20-11	5	VR17-15	5	Casina	6
246.128	5.5	Tonda Romana	5.5	Fusco Rubra	6
Tonda Romana	5.5	233.007	6	Tonda Romana	6
233.007	6	Gem	6	VR17-15	6
Gem	6	VR20-11	6.5	GH88-14	6.75
Fusco Rubra	6.5	Fusco Rubra	7	VR20-11	7

Table A9 Genotype means in the different years for husk length

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
Fusco Rubra	22.86	Fusco Rubra	21.84	Aurea	20.21
Aurea	23.54	Aurea	24.03	Fusco Rubra	21.93
246.128	23.90	VR20-11	24.52	VR20-11	24.12
VR20-11	24.67	246.128	25.40	246.128	24.84
179.043	25.14	225.077	27.42	Contorta	28.35
Contorta	28.51	Contorta	29.89	225.077	28.46
GH140-4	29.00	VR17-15	30.01	Ribet	29.33
166.034	29.16	026.072	30.03	186.080	29.58
VR17-15	29.31	183.060	30.63	RG1	29.68
225.077	29.62	186.080	30.81	179.043	30.01
Ribet	29.74	RG1	30.84	GH140-4	30.77
186.080	30.09	GH140-4	30.88	026.072	31.12
026.072	30.43	166.034	31.64	166.034	31.43
Negret	30.52	Ribet	31.68	Mortarella	31.47
RG1	30.86	179.043	32.03	255.003	32.08
255.003	31.01	Negret	32.44	VR17-15	32.74
Mortarella	31.04	233.007	32.60	183.060	32.92
Segorbe	32.13	Mortarella	32.75	039.044	33.08
Birk5-6	32.86	Birk5-6	33.28	Negret	34.74
039.044	32.87	Tonda Romana	33.53	Tonda Romana	34.94
183.060	33.33	255.003	33.65	Segorbe	35.38
Sant Jaume	34.29	039.044	34.44	055.129	36.27
233.007	34.76	Casina	35.56	162.017	36.36
055.129	34.87	055.129	36.10	Birk5-6	36.40
Tonda Romana	35.38	Segorbe	36.31	TGDL	36.42
Casina	35.84	245.094	36.73	233.007	36.91
TGDL	36.08	TGDL	37.12	Tonda di Giffoni	37.16
245.094	36.15	Sant Jaume	37.69	Casina	37.92
Brixnut	36.42	162.017	37.99	Sant Jaume	38.21
Willamette	37.50	Hall's Giant	38.84	245.094	38.65
162.017	37.57	Willamette	39.24	Brixnut	39.57
Tonda di Giffoni	37.81	Tonda di Giffoni	39.40	Willamette	39.59
244.001	39.39	Brixnut	39.74	GH88.14	39.91
GH88.14	41.39	GH88.14	40.74	Hall's Giant	40.79
Daviana	43.07	054.021	42.30	055.077	41.03
023.017	43.29	Gem	43.58	244.001	42.96
Hall's Giant	43.60	244.001	43.62	Gem	43.42
055.077	45.75	055.077	44.55	054.021	45.67
054.021	46.28	023.017	46.69	Daviana	46.86
Gem	46.33	Daviana	47.23	023.017	47.07
054.039	54.90	054.039	49.75	054.039	47.96

Table A10 Genotype means in different years for relative husk length

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
179.043	1.28	VR20-11	1.32	Aurea	1.17
VR20-11	1.31	Aurea	1.39	VR20-11	1.27
Contorta	1.33	Contorta	1.45	Contorta	1.35
Aurea	1.34	Gem	1.48	Fusco Rubra	1.38
039.044	1.41	039.044	1.49	225.077	1.44
Ribet	1.44	Fusco Rubra	1.49	039.044	1.45
Brixnut	1.49	225.077	1.50	Ribet	1.46
Negret	1.50	Brixnut	1.57	179.043	1.51
Gem	1.51	246.128	1.58	Gem	1.51
Fusco Rubra	1.52	Ribet	1.58	246.128	1.55
Mortarella	1.53	Mortarella	1.61	Mortarella	1.56
225.077	1.53	179.043	1.64	RG1	1.57
Segorbe	1.54	Negret	1.65	255.003	1.59
246.128	1.54	233.007	1.65	186.080	1.60
255.003	1.59	Hall's Giant	1.66	Brixnut	1.62
VR17-15	1.59	VR17-15	1.71	Negret	1.67
RG1	1.63	RG1	1.72	GH88.14	1.70
186.080	1.66	Tonda Romana	1.72	VR17-15	1.70
233.007	1.68	Birk5-6	1.73	Segorbe	1.73
166.034	1.69	GH88.14	1.75	Tonda Romana	1.75
Daviana	1.69	183.060	1.76	GH140-4	1.75
GH140-4	1.70	255.003	1.77	Hall's Giant	1.75
Birk5-6	1.72	Segorbe	1.77	166.034	1.78
Tonda Romana	1.73	186.080	1.80	Daviana	1.78
GH88.14	1.77	Daviana	1.80	Birk5-6	1.79
Willamette	1.78	GH140-4	1.86	Tonda di Giffoni	1.82
Sant Jaume	1.80	055.129	1.86	233.007	1.82
055.129	1.82	166.034	1.87	183.060	1.85
Hall's Giant	1.83	026.072	1.90	162.017	1.90
Tonda di Giffoni	1.83	245.094	1.92	245.094	1.91
245.094	1.84	TGDL	1.97	055.129	1.92
183.060	1.85	Sant Jaume	1.97	Willamette	1.92
TGDL	1.86	Willamette	1.98	TGDL	1.93
026.072	1.92	Tonda di Giffoni	2.00	026.072	1.94
244.001	1.94	Casina	2.05	Sant Jaume	1.97
162.017	2.01	162.017	2.07	Casina	2.03
Casina	2.03	244.001	2.14	244.001	2.08
023.017	2.11	054.021	2.15	055.077	2.14
054.021	2.27	055.077	2.33	023.017	2.25
055.077	2.35	023.017	2.34	054.021	2.31
054.039	2.93	054.039	2.71	054.039	2.57

Table A11 Genotype means in the different years for date of opening of female flowers

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
GH140-4	1	GH140-4	-1	Birk5-6	-1
Negret	1	Negret	-1	GH140-4	-1
Tonda di Giffoni	1	179.043	0	Negret	-0.5
179.043	3.5	Birk5-6	0	Sant Jaume	-0.5
Birk5-6	3.5	Mortarella	1.5	054.039	1
TGDL	3.5	Tonda di Giffoni	1.5	055.077	1
Mortarella	4	055.077	2	162.017	1
Sant Jaume	4	162.017	2.5	179.043	1
054.021	5	Sant Jaume	2.5	186.080	1
054.039	5	054.021	3	Fusco Rubra	1
055.077	5	186.080	3	Mortarella	1
055.129	5	Tonda Romana	3	Tonda di Giffoni	1
162.017	5	Ribet	3.5	VR17-15	1
186.080	5	TGDL	3.5	225.077	1.5
225.077	5	Willamette	3.5	Tonda Romana	1.5
Willamette	5	054.039	4	Willamette	1.5
246.128	5.5	225.077	4	054.021	2
Brixnut	5.5	Fusco Rubra	4	055.129	2
RG1	5.5	055.129	4.5	183.060	2
Segorbe	5.5	Gem	4.5	233.007	2
VR17-15	5.5	VR17-15	4.5	TGDL	2
Fusco Rubra	6	023.017	5	023.017	2.5
Ribet	6	Brixnut	5	Brixnut	2.5
Tonda Romana	6	246.128	5.5	Ribet	2.5
023.017	6.5	183.060	6	Segorbe	2.5
026.072	6.5	244.001	6	VR20-11	2.5
Hall's Giant	6.5	RG1	6.5	245.094	3
VR20-11	6.5	245.094	7	246.128	3
183.060	7	VR20-11	7.5	255.003	3
233.007	7	Segorbe	8	026.072	5
244.001	7	255.003	8.5	166.034	5
245.094	7	Casina	9	244.001	5
255.003	7	Daviana	9	Gem	5
Casina	7	Contorta	9.5	RG1	5
Daviana	7	Aurea	12	Casina	5.5
Gem	7	026.072	13	Daviana	5.5
166.034	7.5	039.044	13	Hall's Giant	5.5
039.044	8	166.034	13	039.044	6
Contorta	8	233.007	13	Contorta	6
GH88.14	9	Hall's Giant	13	GH88.14	6
Aurea	11	GH88.14	14	Aurea	9

Table A12 Genotype means in different years for time of catkin elongation

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
TGDL	1.5	TGDL	1.5	186.080	1
055.077	2	233.007	2	GH88.14	1
186.080	2	GH88.14	2	Sant Jaume	1
GH88.14	2	Segorbe	2	Segorbe	1
162.017	3	186.080	3	TGDL	1
Negret	3	Sant Jaume	3.5	026.072	2
Sant Jaume	3	162.017	4	054.039	2
Segorbe	3	Negret	4	055.077	2
Tonda Romana	3	179.043	4.5	055.129	2
023.017	4	Willamette	4.5	179.043	2
026.072	4	055.077	5	183.060	2
054.039	4	GH140-4	5	225.077	2
055.129	4	Birk5-6	5.5	Birk5-6	2
179.043	4	Brixnut	6	GH140-4	2
225.077	4	Mortarella	6	Mortarella	2
233.007	4	Tonda Romana	6	RG1	2
246.128	4	183.060	6.5	Ribet	2
Birk5-6	4	RG1	6.5	Tonda Romana	2
GH140-4	4	023.017	7	Willamette	2
Mortarella	4	054.039	7	023.017	2.5
RG1	4	246.128	7	162.017	2.5
Ribet	4	255.003	7	246.128	2.5
Willamette	4	Gem	7	Daviana	2.5
183.060	4.5	Ribet	7	Negret	2.5
166.034	5	026.072	7.5	Tonda di Giffoni	2.5
255.003	5	055.129	7.5	233.007	3
Brixnut	5	225.077	7.5	245.094	3
Daviana	5	Tonda di Giffoni	7.5	255.003	3
Tonda di Giffoni	5	VR20-11	7.5	Brixnut	3
Casina	5.5	166.034	8	VR20-11	3
Gem	5.5	Casina	8	Fusco Rubra	3.5
VR20-11	5.5	Daviana	8	Gem	3.5
039.044	6	VR17-15	8	244.001	4
054.021	6	244.001	8.5	VR17-15	4
VR17-15	6	245.094	8.5	054.021	5
244.001	6.5	039.044	9	166.034	5
245.094	6.5	Hall's Giant	11	Casina	5
Hall's Giant	6.5	054.021	12	039.044	5.5
Fusco Rubra	7.5	Fusco Rubra	12	Hall's Giant	6
Contorta	10	Contorta	13	Contorta	8
Aurea	11	Aurea	15	Aurea	9.5

Table A13 Genotype means in the different years for time of leafing out

1994		1995		1996	
GENOTYPE	LSMEANS	GENOTYPE	LSMEANS	GENOTYPE	LSMEANS
054.021	1	055.077	1	Tonda di Giffoni	1
055.077	1	225.077	1	054.039	2
GH140-4	1	GH140-4	1	055.077	2
Sant Jaume	1	Sant Jaume	1	GH140-4	2
Tonda di Giffoni	1	Tonda di Giffoni	1	Sant Jaume	2
026.072	1.5	179.043	1.5	TGDL	2.5
225.077	1.5	TGDL	1.5	026.072	3
Birk5-6	1.5	026.072	2	054.021	3
TGDL	1.5	054.039	2	179.043	3
023.017	2	162.017	2	186.080	3
054.039	2	186.080	2	225.077	3
055.129	2	246.128	2	Birk5-6	3
179.043	2	Birk5-6	2	Tonda Romana	3
183.060	2	Gem	2	Willamette	3
246.128	2	Negret	2	162.017	3.5
Negret	2	Willamette	2	183.060	3.5
Tonda Romana	2	055.129	2.5	023.017	4
Willamette	2	Brixnut	2.5	233.007	4
186.080	2.5	Mortarella	2.5	246.128	4
Gem	2.5	023.017	3	Gem	4
162.017	3	054.021	3	GH88.14	4
233.007	3	183.060	3	Mortarella	4
GH88.14	3	233.007	3	Negret	4
VR17-15	3	Tonda Romana	3	RG1	4
Brixnut	3.5	VR17-15	3	Segorbe	4
Casina	3.5	RG1	3.5	VR17-15	4
Mortarella	3.5	Ribet	3.5	VR20-11	4
Segorbe	3.5	Segorbe	3.5	055.129	4.5
039.044	4	039.044	4	245.094	4.5
166.034	4	166.034	4	Brixnut	4.5
245.094	4	245.094	4	039.044	5
255.003	4	Daviana	4	166.034	5
Contorta	4	Fusco Rubra	4	255.003	5
Daviana	4	GH88.14	4	Casina	5
Fusco Rubra	4	VR20-11	4	Daviana	5
RG1	4	255.003	4.5	Fusco Rubra	5
Ribet	4	Casina	4.5	Ribet	5
VR20-11	4	Hall's Giant	4.5	Hall's Giant	5.5
244.001	4.5	244.001	5	244.001	6
Hall's Giant	4.5	Contorta	5	Contorta	6
Aurea	6	Aurea	7	Aurea	8

Table A14 Estimators of heritability with covariance analysis[z]

Estimation procedure	Parent and progeny evaluation For estimating heritability	Estimator of σ_{cpo}/σ_p^2
1	the same year	$(\sigma_{cpo} + \sigma_{epo}/y) / \sigma_p^2$
2	the different year	$\sigma_{cpo} / \sigma_p^2$

[z] Two estimators were used to calculate heritability in Table A15 by covariance analysis.

Table A15 Comparison of heritability estimation by different methods with pooled data

Trait[Z]	Regression method			Covariance analysis[V]	
	I[Y]	I[X]	II[W]	I	II
	h^2±se	h^2±se	h^2±se	h^2	h^2
NL	0.656±0.055	0.661±0.054	0.665±0.070	0.665	0.663
NW	0.790±0.050	0.765±0.057	0.797±0.064	0.797	0.810
ND	0.904±0.051	0.884±0.053	0.911±0.065	0.911	0.917
NSI	0.559±0.109	0.573±0.111	0.638±0.150	0.641	0.641
NCI	0.920±0.089	0.911±0.091	0.969±0.109	0.955	0.977
NWT	0.636±0.041	0.636±0.039	0.650±0.055	0.650	0.652
KWT	0.663±0.048	0.666±0.050	0.695±0.062	0.694	0.692
%K	0.853±0.082	0.796±0.092	0.873±0.113	0.873	0.903
FA	0.532±0.092	0.510±0.094	0.613±0.111	0.614	0.627
BA	0.648±0.081	0.664±0.079	0.696±0.097	0.696	0.688
DOFF	0.576±0.052	0.492±0.063[U]	0.621±0.066	0.621	0.670
TCE	0.677±0.048	0.584±0.064[U]	0.689±0.064	0.689	0.739
LO	0.724±0.049	0.728±0.048	0.756±0.060	0.756	0.754

[Z] The calculation of heritability for the former 10 traits was based on 29 progenies, while the later 3 traits based on 35 progenies.
[Y] Regression data points were from the same year, i.e. regression of 1995 progeny means on 1995 midparent values, and 1994 progeny means on 1994 midparent values.
[X] Regression data points were from the different year, i.e. regression of 1995 progeny means on 1994 midparent values, and 1994 progeny means on 1995 midparent values.
[W] Regression data points were from the average in the two years.
[V] Covariance analysis used estimation procedures 1 and 2 in Table A14 to calculate heritability for traits.
[U] There was no common slope between two separate data sets.

Table A16 Comparision of heritability estimation by different methods with a single year's data set (balanced data)

Trait[z]	Progeny 1994 Midparent 1994	1995 1995	1994 1995	1995 1994
NL	0.682±0.076	0.628±0.080	0.728±0.078	0.601±0.072
NW	0.831±0.073	0.790±0.050	0.850±0.084	0.687±0.075
ND	0.913±0.078	0.895±0.073	0.885±0.073	0.882±0.079
NSI	0.581±0.155	0.532±0.162	0.684±0.171	0.480±0.144
NCI	0.852±0.135	0.993±0.131	0.989±0.114	0.840±0.142
NWT	0.651±0.058	0.621±0.055	0.628±0.060	0.638±0.054
KWT	0.669±0.071	0.657±0.073	0.666±0.065	0.667±0.076
%K	0.845±0.110	0.862±0.096	0.847±0.128	0.751±0.132
FA	0.584±0.132	0.440±0.154	0.695±0.188	0.405±0.086
BA	0.667±0.131	0.626±0.121	0.807±0.124	0.541±0.097
DOFF	0.628±0.086	0.560±0.070	0.325±0.049	1.063±0.123
TCE	0.696±0.065	0.670±0.071	0.386±0.052	1.106±0.109
LO	0.763±0.084	0.695±0.057	0.675±0.066	0.799±0.071

[z] The calculation of heritability for the former 10 traits was based on 29 progenies, while the later 3 traits based on 35 progenies.

Table A17 Variance components of 17 traits in hazelnut for pooled data with Type I method

Trait	G	T(G)	Y	Y x G	T(G) x Y	Error
NL	7.578	0.092	0.062	0.098	0.073	1.121
NW	3.819	0.027	0.557	0.292	0.142	0.830
ND	4.624	0.049	0.275	0.190	0.118	0.662
SI	0.01087	0.00014	0.00051	0.00053	0.00015	0.00290
CI	0.00260	0.00005	0.00010	0.00017	0.00010	0.00283
NWT	47.586	1.444	3.197	7.044	2.509	1.821
KWT	7.997	0.168	1.069	1.343	0.509	0.378
%K	0.00205	0.00003	0.00005	0.00008	0.00008	0.00007
FA	0.414	-0.006	0.046	0.092	0.138	0.011
BA	2.436	0.028	0.098	0.197	0.138	0.157
NNPC	0.237	0.020	0.021	0.063	0.013	0.053
HL	38.187	1.304	0.172	0.776	2.152	9.929
RHL	0.06336	0.00097	0.00136	0.00084		0.00811
NM	2.666	-0.085	0.406	0.708		0.757
DOFF	6.025	0.094	2.868	2.301		0.599
TCE	3.982	0.063	0.707	0.820		0.264
LO	1.524	0.038	0.371	0.104		0.135

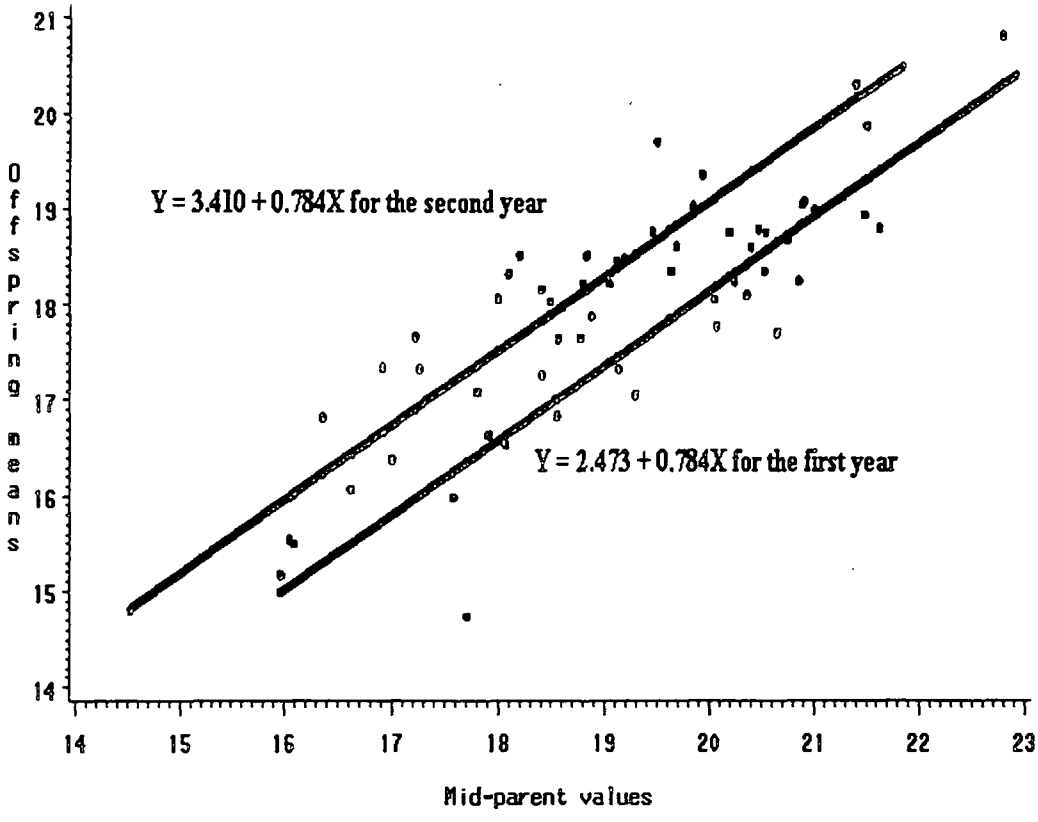

Figure A1 Regression of offspring means on mid-parent values for nut width

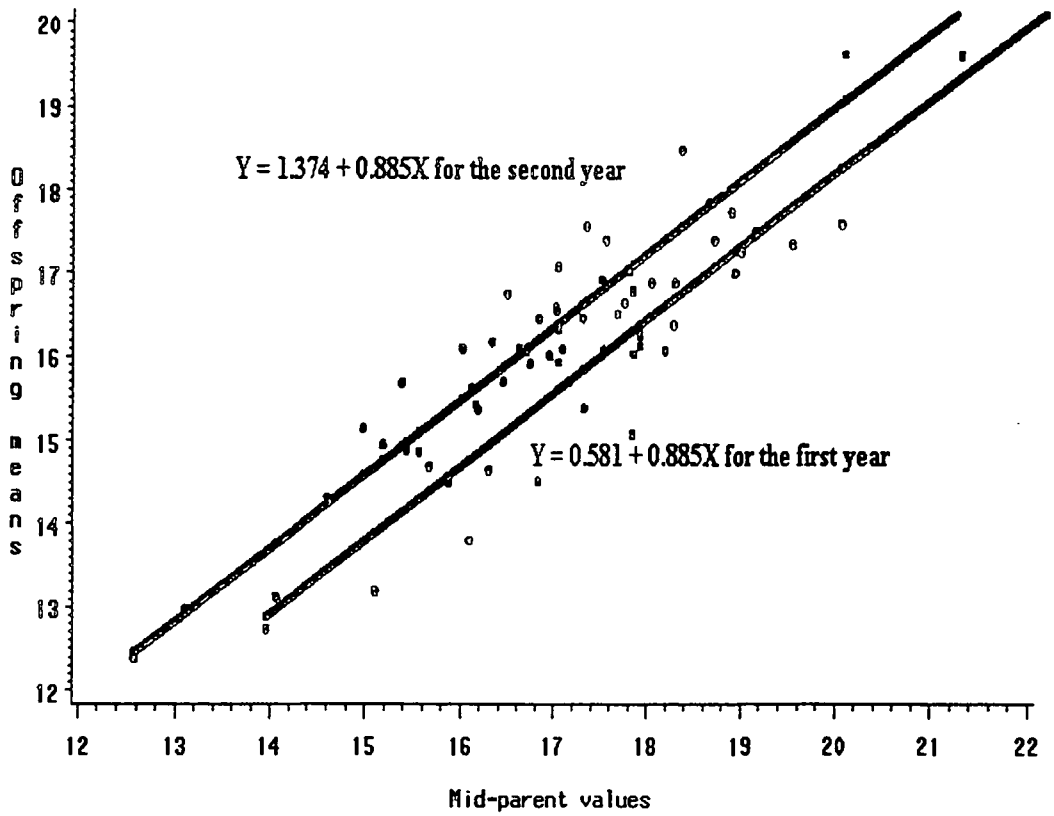

Figure A2 Regression of offspring means on mid-parent values for nut depth

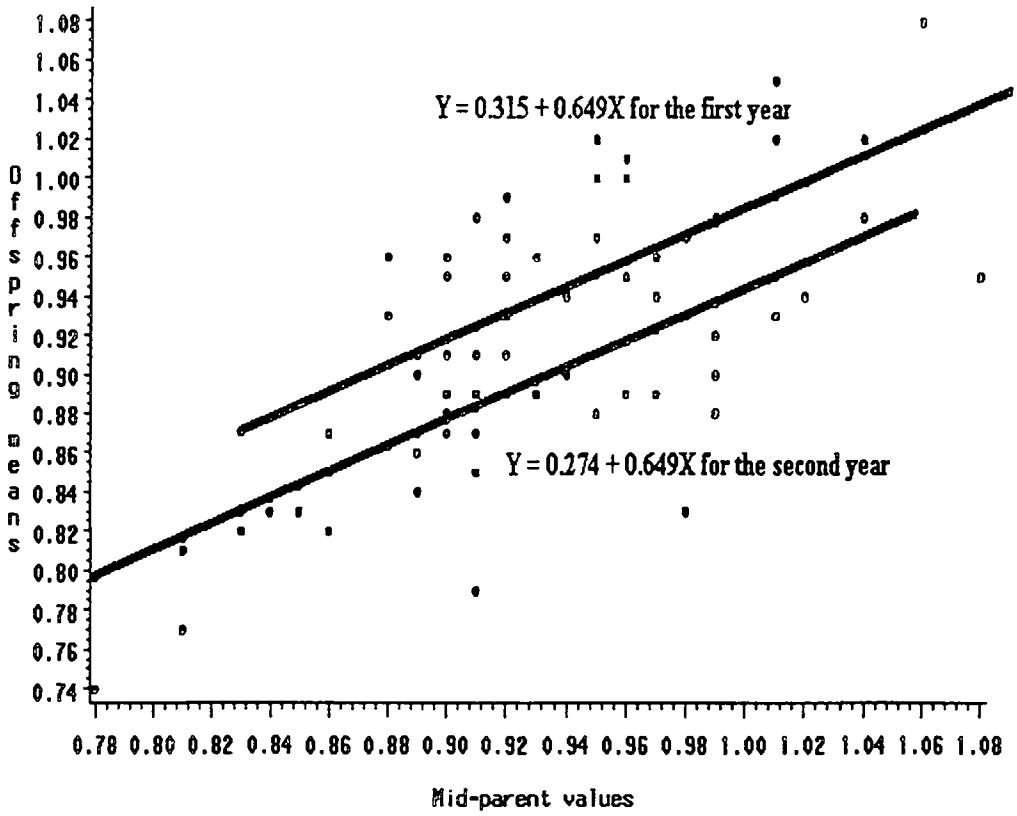

Figure A3 Regression of offspring means on mid-parent values for nut shape index

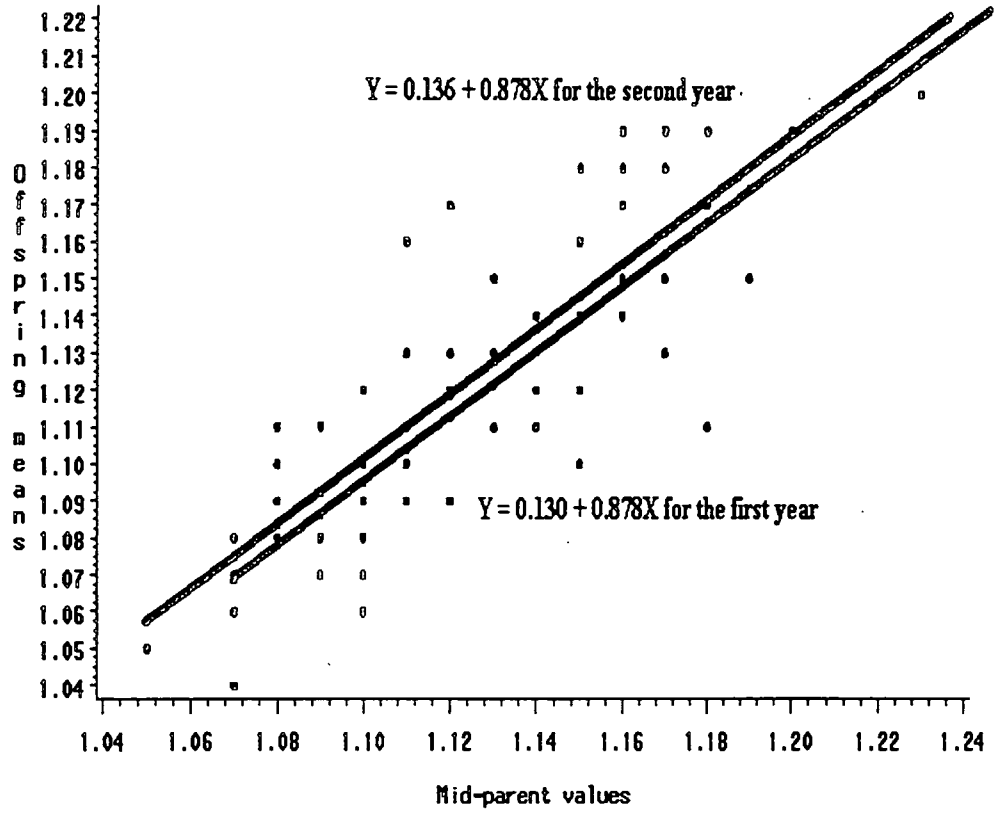

Figure A4 Regression of offspring means on mid-parent values for nut compression index

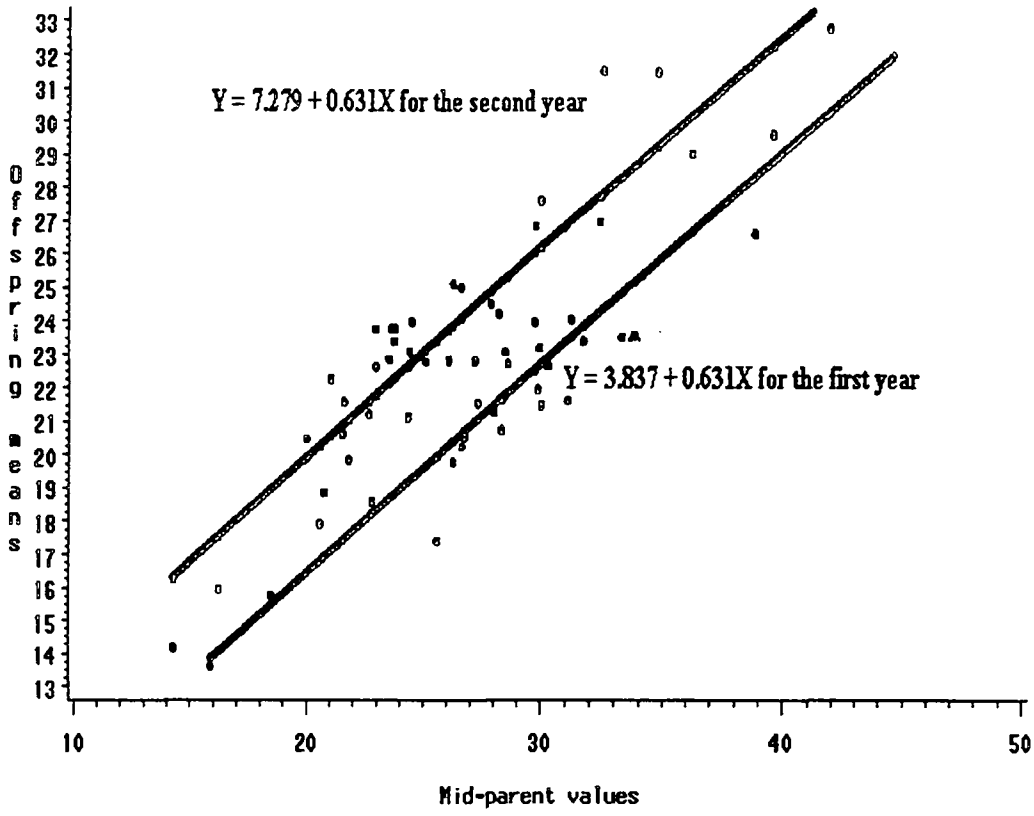

Figure A5 Regression of offspring means on mid-parent values for nut weight

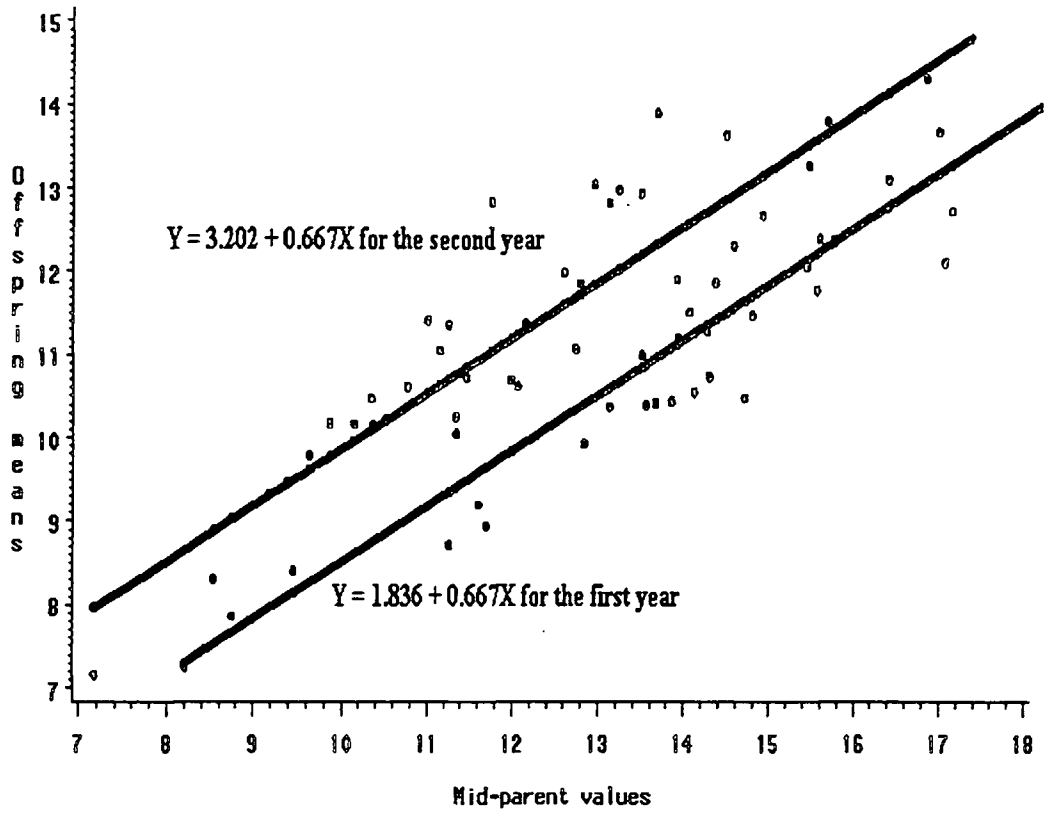

Figure A6 Regression of offspring means on mid-parent values for kernel weight

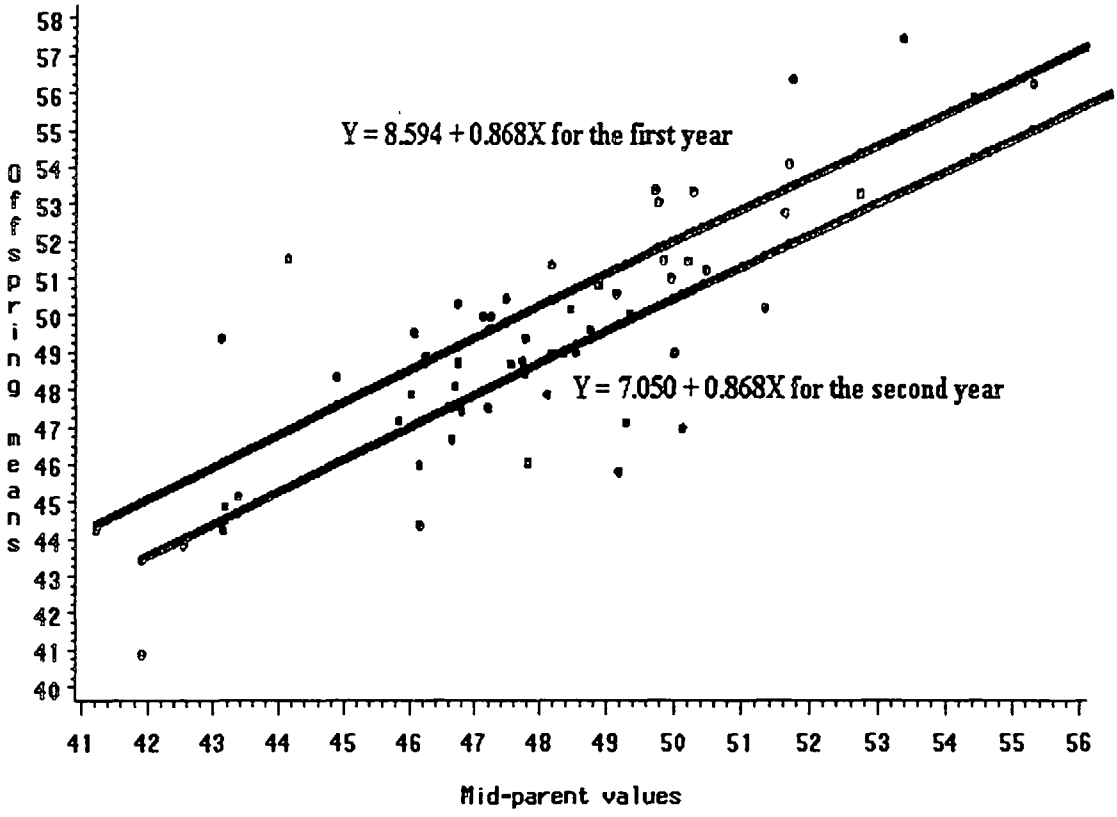

Figure A7 Regression of offspring means on mid-parent values for % K

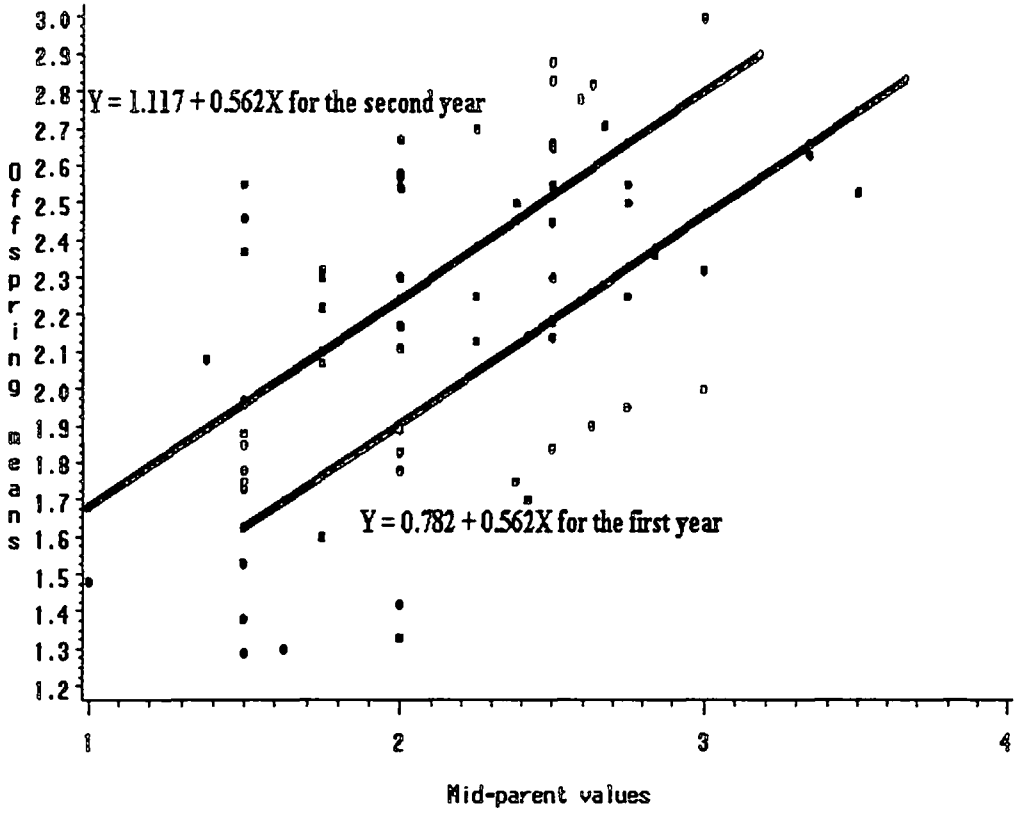

Figure A8 Regression of offspring means on mid-parent values for fiber amount

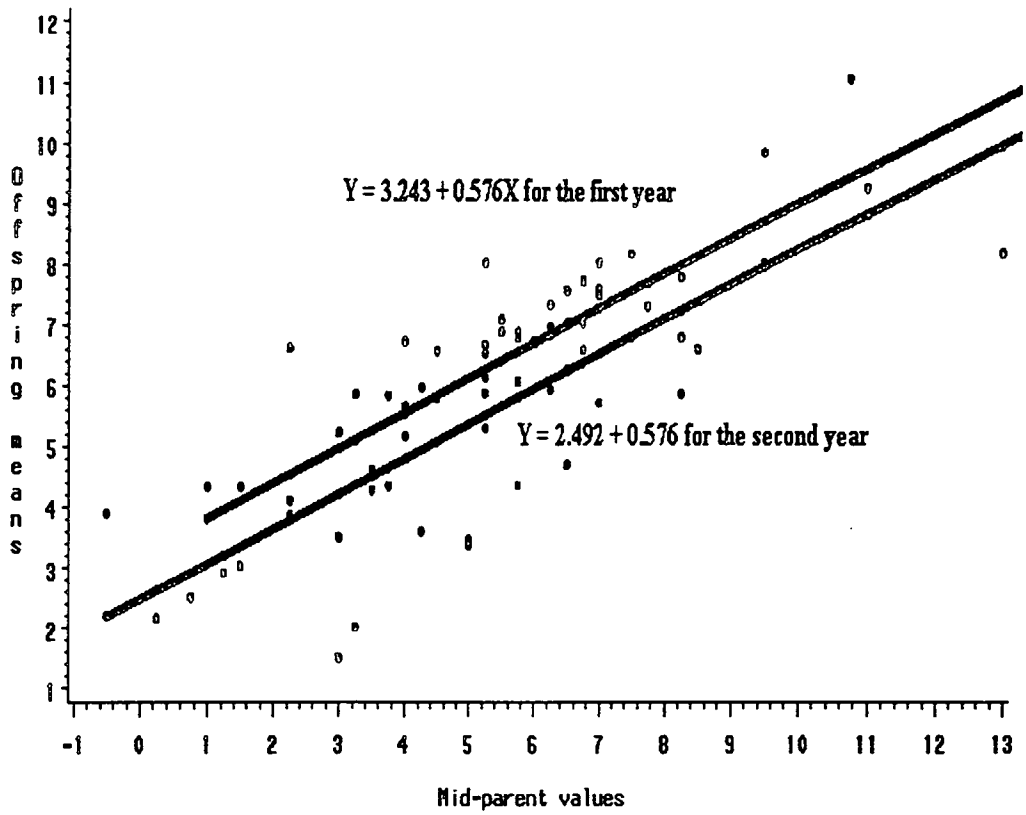

Figure A9 Regression of offspring means on mid-parent values for date of opening of female flowers

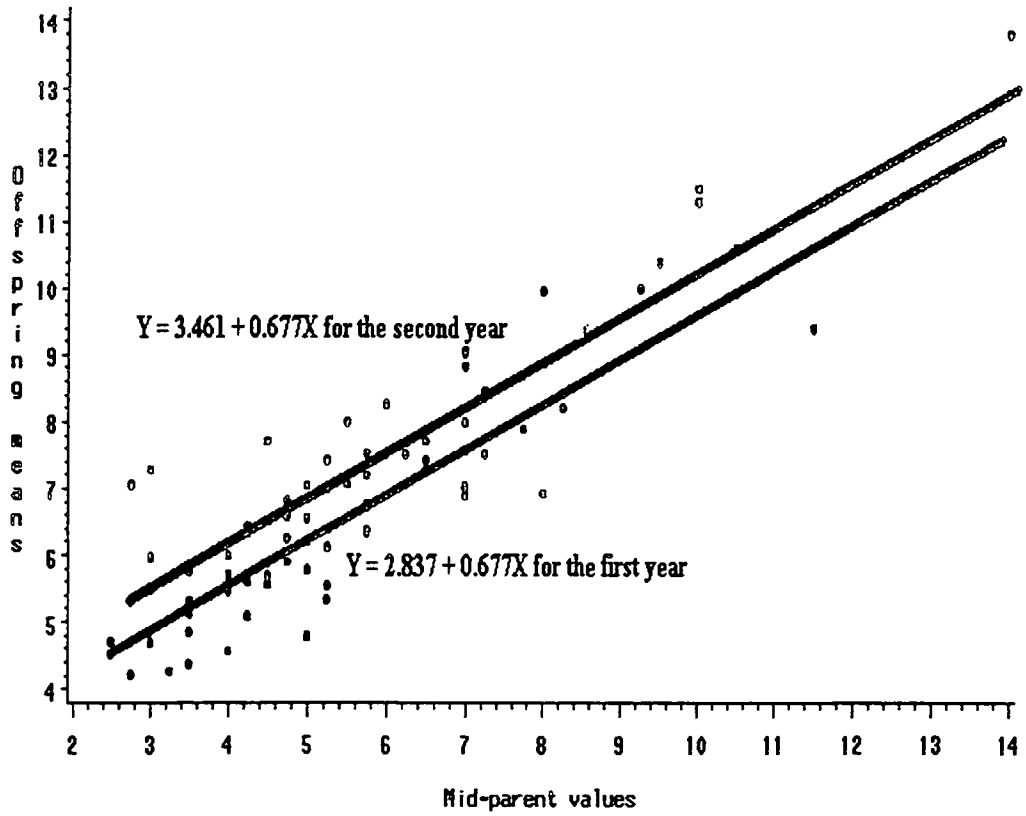

Figure A10 Regression of offspring means on mid-parent values for time of catkin elongation

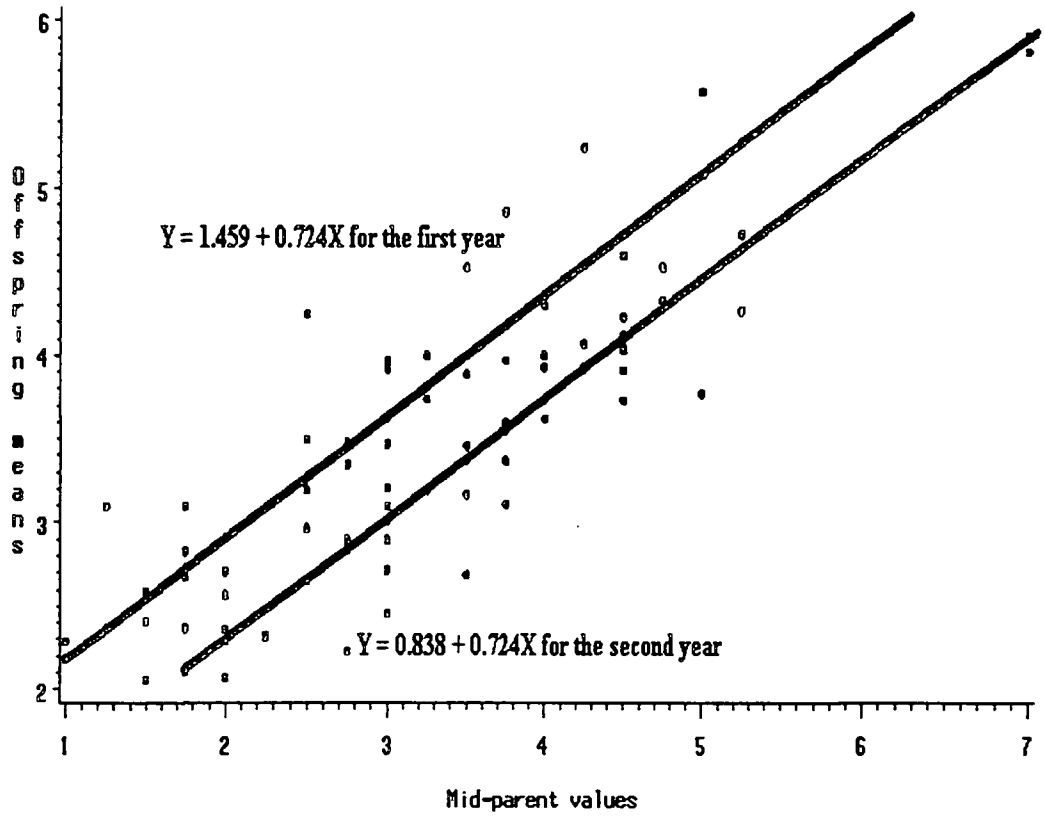

Figure A11 Regression of offspring means on mid-parent values for leafing out