INBREEDING IN DIPLOID AND AMPHIDIPLOID *DENDROBIUM*

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN HORTICULTURE

DECEMBER 1981

By

Carol Akie Bobisud

Dissertation Committee:

Haruyuki Kamemoto, Chairman
Richard Hartmann
Henry Nakasone
Yoneo Sagawa
James Silva

We certify that we have read this dissertation and that in our opinion it is satisfactory in scope and quality as a dissertation for the degree of Doctor of Philosophy in Horticulture.

DISSERTATION COMMITTEE

Chairman

ABSTRACT

Nine inbred progenies derived from amphidiploid Dendrobium Jaquelyn Thomas 'Y166-1' and one noninbred progeny were studied. Selfings, sibmatings and backcrosses were done using individuals randomly chosen or selected for larger flowers having a low amount of pink tinge on the white petals and sepals. Vigorous plants of each progeny were selected for cultivation. Selection coupled with inbreeding was successful in increasing flower size and decreasing the degree of pink tinge. This process of selection and inbreeding effected a decline in yield (number of harvested racemes) from the S_1 to the S_3. Inbreeding decline was not apparent in the characters of scape length, raceme length, number of initiated flowers per raceme, percent bud drop and vase life; the genetic constitutions of the parents seemed to determine the nature of these characters in the progeny. It was not clear to what extent inbreeding affected shoot height.

Dry weight measurements were taken for progenies from selfing D. d'albertsii, D. schulleri, D. phalaenopsis and D. Jaquelyn Thomas. Plants were dried and weighed when in the flask stage of growth and a mean plant dry weight was calculated for each flask. No inbreeding depression was observed in progenies of five generations of selfing a diploid D. d'albertsii. Due to a tendency of the protocorms to proliferate, it was difficult to assess any difference among the D. schulleri inbred progenies. Inbred progenies of amphidiploid D. Jaquelyn Thomas '2085-4N' and amphidiploid D. Jaquelyn Thomas

'Y166-1' did not display inbreeding decline. Two S_2 progenies of D. phalaenopsis 'Kosaki' gave significantly lower dry weight measurements than the S_1 progeny while one S_2 progeny did not differ from the S_1.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Dendrobium orchids are developing into an important cut flower crop in Hawaii. Dendrobium cultivars grown for cut flower production have been derived from intersectional crosses involving the Phalaenanthe and Ceratobium sections within the genus Dendrobium. Dendrobium Jaquelyn Thomas 'Uniwai Blush' (also known as UH44), introduced by the University of Hawaii, is the first seed-propagated amphidiploid dendrobium cultivar. It is a hybrid of D. phalaenopsis of the Phalaenanthe section and D. gouldii of the Ceratobium section.

Favorable characteristics of 'Uniwai Blush' are a high number of racemes produced, a low incidence of bud drop on the racemes and a long vase life of the cut racemes. The flowers of this cultivar are basically white but possess a conspicuous pink tinge. A more attractive raceme is one with larger, whiter flowers. Selection of extreme individuals exhibiting large flower size and a low amount of the pink tinge and inbreeding these plants may result in offspring having flowers of larger size and a lighter pink tinge in comparison to that of 'Uniwai Blush'. However, inbreeding may result in a decline in vigor. An associated decline in some characters (such as yield) may render an inbred cultivar undesirable for commercial cropping despite an improvement in flower size and color. Therefore, this study was initiated to determine if increases in flower size and color purity can be obtained through selection, and if inbreeding negatively affects desirable characters.

Inbreeding effects are often detected at the mature stage of the progenies. Orchid plants have a relatively long life cycle. It takes about three years from germination to the first bloom; an additional two to four years are required to evaluate yield and other floral characteristics. It would facilitate breeding research if decline through inbreeding can be detected at an early seedling stage. Accordingly, a second experiment was initiated to determine inbreeding effects at the seedling stage in aseptic culture on three diploid Dendrobium species and two amphidiploid Dendrobium Jaquelyn Thomas hybrids.

LITERATURE REVIEW

Inbreeding

Many wild species and cultivated varieties naturally self-pollinate, and the offspring appear to suffer no ill effects in terms of vigor, productiveness, and ability to survive. However, the majority of higher plants possess devices which promote cross-pollination. These naturally cross-pollinated plants, when artificially inbred, tend to display injurious effects. Most plants seem to benefit favorably from cross-fertilization (East and Jones, 1919).

East and Jones (1919) and Jones (1925) defined inbreeding in terms of limited parentage. The manner in which individuals are mated is the basis of the idea of inbreeding. Pearl, cited by East and Jones (1919), defined inbreeding as " . . . a narrowing of the network of descent as a result of mating together at some point in the network of individuals genetically related to one another in some degree."

Darwin (1900) experimented with inbreeding and crossbreeding. Ipomoea purpurea and Mimulus luteus, the two species which were inbred the longest, showed sensitivity to inbreeding. Yet in each species plants did appear that were more vigorous than the other inbred plants from the same stock and equalled or surpassed the vigor of the original cross-pollinated stock. Segregation of the inbred stock occurred and resulted in different types with different visible hereditary characters and differing in the ability to grow. The inbred plants were also observed to be more uniform in visible characters than the

original cross-pollinated stock. Darwin concluded that cross-fertilization generally had beneficial effects while self-fertilization was frequently injurious.

Shull (1908) observed that rows of self-fertilized maize differ from one another in definite characters. He concluded that these differences are not an effect of inbreeding in itself but a result of inbreeding due to an isolation of biotypes from complex hybrid combinations. In comparing cross-fertilized and self-fertilized strains of the same origin, vigor of the biotypes and their hybrids rather than the effects of the processes of inbreeding and crossbreeding are being noted. The observations of greater vigor of the cross-fertilized strains prompted Shull's suggestion that continuous hybridization rather than the isolation of pure types be the direction of the corn breeder.

Shull (1910) later modified this hypothesis to encompass the concept that although vigor in hybrids can generally be attributed to heterozygosity, in some elements the heterozygous state can be without vigor or even depressing.

East (1908) worked with two types of maize: a smooth, full kernel type and a type with a thin, peaked kernel. Crosses of plants of the same type resulted in the accentuation of type characters. Crosses between types were more vigorous and yielded more than crosses within types.

East (1908) questioned the theory of accumulation of deleterious characters being responsible for the bad effects of inbreeding. In maize the injurious effects of inbreeding were no less common when

superior instead of inferior parents were involved. Also, different selfed strains from the same original stock displayed extremes of characters, such as wide or narrow leaves and tall or short stems, both of which extremes could not be attributed to merely the self-fertilization process. Therefore, deterioration must be an indirect consequence of inbreeding.

East (1909) further argued that although there were many examples of deterioration resulting from inbreeding, there were also cases of superior inbred stock. Hence, the deterioration was made possible by the process of inbreeding but was not a direct consequence of it. Since not all species naturally cross-fertilize, inbreeding and a decrease in vigor cannot be conclusively linked as cause and effect.

Naturally crossbred species, when inbred, tend to isolate into types which are homozygous and so lack the stimulus derived from free intercrossing and appear to deteriorate. East (1909) noted that this deterioration is in no way a degeneration of hereditary characters in corn but is solely manifested in plant size and yield. Thus, this type of degeneration is a partial loss of development and decrease in cell division.

Two effects of crossbreeding are: a recombination of hereditary factors and a stimulation to development. East (1909) postulated that when two differing gemetic constitutions are combined, there is an increase in stimulation of growth. Such a hypothesis accommodates the observations of decrease in vigor without the degeneration of characters. This theory also explains why this decline in vigor reaches a limit with the attainment of a completely homozygous individual.

Shull (1911) ran extensive studies comparing self-fertilized and cross-fertilized Indian corn. His major observations were: 1) progeny of self-fertilized parents were inferior to those of cross-fertilized parents in respect to height, yield and other characters with a basis in physiological vigor, and 2) each self-fertilized family was distinguishable from other such families by particular, distinct morphological characters. Within each self-fertilized family a uniformity of these morphological characters among the individuals was apparent.

Shull (1911) also presented what he considered proof that the self-fertilized families of the same original stock were genotypically distinct and not fluctuations of the same genotype. In a population in which the mean number of ear rows was slightly above 14 rows, selection was practiced for 12 and 14 rows. The mean number of rows in the 12-row family shifted to a lower number than that selected (further generations approached 8 rows) while the 14-row family remained with a mean of 14. Since all plants were grown under nearly uniform conditions, Shull concluded that internal rather than external factors were involved. As inbreeding continued, the self-fertilized lines decreased in variability of row number.

The idea that inbreeding in itself is injurious was rejected by Shull (1911). He conceded that if such injury were real it was insignificant relative to the great vigor shown by the heterozygous condition. Further supporting evidence was that continued self-fertilization in any line did not produce the corresponding decrease in size and vigor in every generation. The decrease in the

second year of self-fertilization was not as great as that observed in the first year, in the third year still less was noticed and a limit was approached as self-fertilization continued. This supported Shull's hypothesis that when complete homozygosity is achieved no further deterioration ensues and so self-fertilization itself cannot be injurious.

In accordance with the view that the degree of vigor is due to the degree of hybridity, certain inferences were made (Shull, 1911). 1) A cross between two plants of the same self-fertilized family, or the same genotype, will show no increase in vigor over the self-fertilized plants since no new hereditary factors are introduced. 2) A cross of two individuals of different self-fertilized lines, or pure genotypes, will produce first generation hybrids exhibiting the highest degree of vigor since they are heterozygous for the characters which differentiated the parental genotypes. 3) Sib crosses among the first generation hybrids will result in progenies with the same characters, vigor, and degree of heterogeneity as progenies resulting from selfing first generation hybrids.

In Shull's (1910) experiments, yield of F_1 hybrids of certain self-fertilized lines of maize exceeded that of the original cross-pollinated stock. The "injurious effects" of five years of inbreeding were lost through cross-fertilization. Shull attributed the high yield and crop quality of a hybrid of two inbred strains could be repeatedly obtained by remaking the cross. When F_2 hybrids were produced, they exhibited greater variability than the F_1 and this increased variability translated into a decrease in yield.

Jones (1924) as well as Shull (1911) recognized that when selection favors the most vigorous individuals of an inbred generation as progenitors of the subsequent generation, the approach to complete homozygosity is slowed. Jones emphasized that when single individuals are the progenitors of successive inbred generations, the results are dependent upon the genotypes of these individuals.

Jones (1918) found that inbreeding maize reduced the number of nodes per plant, but this decline was much less than that for height and length of ear. He observed that the number of rows per ear increased in some lines and decreased in others. He concluded that inbreeding greatly affects some characters and not others and that segregation had occurred in his plants. The extent to which variability was reduced differed among the lines.

Despite the decline in the size, general vegetative vigor and productiveness as well as greater difficulty in growing them, Jones (1918) found these inbred plants to be normal and healthy. The abnormalities commonly found in a field of maize, such as seeds found in tassels, anthers found in ears, dwarfness, sterility, mosaic and albino plants were never observed in the inbred strains. However, he was impressed by the uniformity in the size, shape, structure and position of the leaves, tassels, stalks and ears.

East and Hayes (1912) reported that normal strains with particular hereditary characters that classify them as degenerate did appear sometimes, but infrequently. They proposed that abnormalities

may arise from strains lacking vigor where cell division does not occur normally.

No particular character is common to all inbred strains. The general manifestations are a loss in vigor, size and productiveness with the appearance of unfavorable characters. Such characters were never found in the same strain (East and Hayes, 1912).

East and Hayes (1912) described the developmentally weak types produced by inbreeding as those which cannot be perpetuated, are difficult to propagate and cannot complete normal development or are normal, but differ in amount of growth at maturity. After the reduction in vigor has essentially ceased, these normal, homozygous, inbred strains are comparable to self-fertilized species.

In 1939 Jones summarized 30 generations of self-fertilization in three lines of maize. Reduction in height stabilized after five generations while yield decline ceased after twenty years. Sib lines which had been separated at different points differed in some instances and not in others. Jones attributed these differences to "spontaneous transmissible variations" and not to delayed segregation. Uniformity and constancy for all visible characters were attained after twenty generations of self-fertilization as well as homozygosity for loci contributing to hybrid vigor. No variations appeared that could be construed as favorable to survival.

Inbreeding studies on alfalfa (Tysdal et al., 1942) showed a general decline in yield as the lines became more inbred. In the S_1 the average of 54 lines showed forage yield to be 68% of that of the original open-pollinated varieties while seed yield decreased to

62%. In the seventh generation of self-fertilization the forage yield was reduced to 26% where it essentially leveled off. Seed yield in the eighth generation of inbreeding was 8% of the original open-pollinated varieties. There was great variability among the selfed lines in both seed and forage yield. In the S_1 lines forage yield ranged from 26 to 105% of the yield of the original varieties.

The inbreeding process is of value in plant improvement to eliminate abnormal, pathological, and generally unfavorable characters since when such characters appear selection can be practiced. Loss of vigor, size and productiveness results from inbreeding. However, uniform, vigorous, productive offspring are obtained when two inbred strains free of unfavorable recessives are crossed (Jones, 1918).

An hypothesis was developed by Balint (1976) resulting from experiments involving a single maize plant. While an increase in recessive, deleterious genes in the homozygous state is an accepted explanation, the formation of defective mutant genes is another factor contributing to inbreeding degeneration. Selfing resulted in metabolic changes which affected nutrient uptake, synthesis and translocation. This was detrimental to development of the seeds and resulted in chromosomal aberrations in the plants grown from the seeds as well as in morphological mutants.

Balint (1976) has stated that since the work of East and Jones, which appeared in 1919, and that of Fisher in 1949, no major advances have been made in the theory of inbreeding. Dorsman (1976) has likewise declared the problem of inbreeding depression, crucial in

hybrid breeding of cross-pollinated crops, to be a sorely neglected field of research which needs to be approached from a physiological side.

Much theoretical work, based on models, has been done regarding inbreeding. Gene fixation in sexual organisms can come about by two mechanisms--selection and inbreeding (Carson, 1967). Wright (1921) attributed the effects associated with inbreeding (increase in uniformity, degeneration of vigor, etc.) to an increase in homozygosity. He introduced a general formula to calculate the theoretical percentage of homozygosity in a diploid organism resulting from inbreeding: this was called the inbreeding coefficient (Wright, 1922).

With inbreeding, the proportion of homozygotes in the population increases. Mutation will generally not be important in causing heterozygosity in inbred populations. However, selection for homozygotes or heterozygotes will speed or slow the progress of inbreeding. If the attainment of homozygosity is desired in a breeding program and there exists a disadvantage of homozygotes, the inbreeding should be as close as possible and the inbreeding should not be interrupted by a looser mating system. Thus, even with close inbreeding, Hardy-Weinberg proportions, due to homozygote disadvantage, may be observed in a population (Hayman and Mather, 1953).

Selection against homozygotes at loci where fixation of any allele causes a reduction in fitness would slow the rate of progress toward homozygosity, both at the loci involved and other loci linked to them. Intense selection against homozygotes at a few points on

the chromosome could greatly reduce the approach to fixation under inbreeding. As inbreeding progresses, the number of loci affected and the severity of this selection may possibly increase such that the average progress toward fixation would lag further and further behind the theoretical level indicated by an increasing inbreeding coefficient (Reeve, 1957).

In an approximately pure line, heterozygosity may exist due to retention of some of the heterozygosity of an original ancestor or because one allelomorph arose from mutation, but, generally, most plants in a pure line are completely homozygous (Haldane, 1936).

Carson (1967) viewed an increase in the mating of relatives as increasing the degree to which gene frequencies are dispersed among inbred lines. This dispersion of gene frequencies is a consequence of small population size, where random drift operates, as well as of inbreeding. Inbreeding is an important force in evolution since dispersion results and it allows for gene fixation, interdeme selection and species formation.

Genetics of inbreeding populations

Since self-pollinating and cross-pollinating plant species generally do not breed exclusively by one or the other system, the inbreeding depression exhibited by normally cross-pollinated plants may be better understood in relation to the question of self-pollinating species.

Stebbins (1957) proposed two explanations for the evolution of self-fertilizing species: 1) an accidental occurrence whereby the

cross-fertilizing capability was lost and hence, a few genotypes managed to survive despite usual inbreeding effects, and 2) the effect of natural selection favoring self-fertilizers under certain conditions. Self-fertilizers were concluded to have originated from cross-fertilizers based on the following reasons: 1) more specialized morphological features than in cross-fertilized relatives are noted, 2) structures advantageous for cross-fertilization persist in some self-fertilizing species, the genes responsible for them not having been modified in the process of changing to self-fertilization, 3) historical evidence of some self-fertilizing species or populations arising from cross-fertilizers, and 4) self-incompatible species of the same family or related families usually have a similar genetic basis for the self-incompatibility. Self-fertilization in certain plants may have originated due to 1) unfavorable conditions for cross-fertilization, such as weather changes or absence of pollinating insects, 2) long distance dispersal, which necessitated self-fertilization for perpetuation, or 3) colonization of new habitats (adaptive, homozygous, self-fertilizing individuals being able to rapidly build up large populations).

Stebbins (1957) saw the population structure of self-pollinating species as being made up of biotypes, genetically homozygous pure lines. Self-fertilization isolates each biotype from another of the same species with which it grew sympatrically. Occasional crossing between biotypes allows for gene exchange to occur. Morley (1959) elaborated that the variation within natural populations of predominantly inbred species is not necessarily far less than that of

self-incompatible species; populations of cross-fertilizing species show a continuous distribution in the characters while in population of self-fertilizers, the variation is bound up in certain combinations.

In self-pollinating agricultural plants, it has been noted since the earliest times that a great store of genetic variability exists (Allard et al., 1968). Old "land" varieties of self-pollinated crops are known to possess great genetic diversity (Allard and Jain, 1962).

After eighteen generations of self-fertilization in a composite-cross population of barley, a predominantly self-pollinated species, an enormous amount of variability was retained. This variation was not only due to different homozygous lines but also due to segregation within families, possibly due to heterozygote advantage. While variation is usually greater between families than it is within families of inbreeding populations, significant variation can exist within families if natural selection for heterozygotes exists (Allard and Jain, 1962). At several marker loci, the decline in heterozygosity after 18 generations did not correspond to the observed levels of selfing and outcrossing. Thus, the genetic variability existent after 18 generations was not only attributable to low levels of outcrossing but also to the substantial heterozygote advantage. It was argued that in self-pollinated plants, this high heterozygote advantage substitutes for a high degree of outcrossing, self-pollinators not necessarily giving up the advantage of heterozygosity (Jain and Allard, 1960).

However, Thompson and Rees (1956) concluded from work on inbred rye that natural selection does not favor heterozygotes per se but

rather certain heterozygous combinations; hence, heterozygosity in itself does not necessarily have a selective advantage.

The variation among natural populations of wild oats, another predominantly self-pollinated species, from three regions in California was found to be based on differences between regions, between sites within regions and from plant to plant within sites. Such geographical differentiation was interpreted as permitting adaptation to the habitats. Estimates of outcrossing ranged from 1 to 12 percent. Substantial variability within families originating from a single plant from the population was found; this was most likely due to heterozygosity at many loci. Hence, the genetic system of wild oats was determined to allow for ongoing change in the gene pool, differing only in degree from outbreeding species, while also providing for superior homozygous genotypes adapted to specific habitats (Imam and Allard, 1965).

A great amount of genetic variability was also found in the Festuca microstachys complex. Variation was found to occur from place to place, within a site and within a single species at a site. It was estimated that the amount of variability within the fescues is no smaller than that of wild oats, a species possessing a many times greater level of outcrossing. The natural population was determined to consist of a very large number of different genotypes, each represented by a few individuals and each homozygous at many loci. Occasional outcrossing allows new genotypes to be introduced into the population and by natural selection are eliminated or incorporated into the system. The population structure is such that the interactions

are at the level of individuals and there is an integration of a large number of genotypes (Kannenberg and Allard, 1967).

Studies have been done on natural selection on populations; two are considered. Four pure lines of barley, when grown in a mixture for 16 years, resulted in one pure line dominating the population; hence, natural selection can be seen to act with great intensity under population conditions (Suneson, 1949). Bulk hybrid populations of rice grown for eight generations in 3 different environments showed different character changes, not the same for different environments. However, the populations in all 3 locations remained quite variable for all characters; thus, natural selection was seen as preserving many different genotypes and not increasing uniformity within the population (Adair and Jones, 1946).

Therefore, there is great genetic diversity in natural and domestic populations of inbreeding species. Many different genotypes exist within such a population, frequently heterozygous at many loci. Clinal variation is due to genetic differentiation, reflecting adaptations to different habitats. The concept of heterozygote advantage helps to explain stable polymorphisms observed under such heavy inbreeding. The existence of many homozygous types in the Festuca microstachys complex may relate to a complex pattern of interactions among the genotypes. Such high genetic variability found within inbreeding populations suggests that such variation is necessary to the survival of populations, any restriction on this variability must be compensated by change in other components if the population is to survive (Allard et al., 1968).

Heterosis

Since heterosis can be viewed as a phenomenon at the opposite extreme of inbreeding depression, insight into inbreeding decline may be gained by studying heterosis.

Animal breeders were first to link the effects of inbreeding with hybrid vigor, regarding hybridity to be the antidote to inbreeding effects (East and Jones, 1919).

Hybrid vigor, no doubt, was observed prior to being recorded in scientific literature. According to Zirkle (1952), Koelreuter published his work on plant hybridization from 1761 to 1766 in which hybrid vigor was first described. He observed floral mechanisms favoring cross-pollination and regarded them to be nature's design for ensuring crossbreeding.

Other botanists followed to record the effects of crossbreeding as well as to describe the mechanism for assuring it (Zirkle, 1952). Among them were Sprengel, who in 1793 accurately detailed the structure of flowers and showed the general avoidance of self-pollination, and Knight who in 1799 attributed hybrid vigor to outcrossing and thus developed an anti-inbreeding principle. Gartner, in 1849, noted the hardiness of many hybrids. Darwin's careful and extensive work was the forerunner of twentieth century research on hybrid vigor.

East and Jones (1919) described the manifestations of hybrid vigor as commonly being a general increase in size. This largeness is due to an increase in the size of the component parts rather than an increase in the number of parts. In maize, for example, the

increase in length of the internodes is much greater than the increase in the number of internodes. Other expressions of vigor in maize include extensions in the diameter of the stalk, increased length and breadth of leaves, greater root development, larger tassels and ears, increased number of ears, and increased seed production. Jones (1918) attributed this increase in size to an increase in both size and number of cells.

East (1936) defined hybrid vigor in terms encompassing the whole organism, plant or animal. In plants its effect is likened to adding a balanced fertilizer to the soil. This vigor is not too apparent in flowers or fruits since the general vegetative stimulus is weakened by the time sexual maturity is reached. Also, reproductive processes and vegetative growth are separate phenomena. Yet preparation for reproduction involves vegetative growth, and hence hybrid vigor is often shown in the profusion of flowers and fruit.

Richey (1946) defined hybrid vigor as "an excess of vigor of a hybrid over the average vigor of its parents."

The term "heterosis" was proposed by Shull (1914) to describe the increased development which may be due to heterozygosity. The term was coined for the sake of brevity and for the want of a word free from implications of Mendelian genes necessarily stimulating the cell division, growth, and other physiological processes of an organism.

Shull (1948) later elaborated upon the scope and generality of the term. The visible and invisible phenomena resulting from the union of different gametes cannot be separated so heterosis applies to

the entire process. The term also includes the differences in uniting gametes not due to analyzable Mendelian genes. Heterosis is more inclusive than hybrid vigor--all hybrid vigor can be termed heterosis but not all heterosis is hybrid vigor (as in certain groups of fungi where unlike elements are brought together by nuclear migrations and not by cross-fertilization). The phenomenon of heterosis is complex and no single mechanism or cause can be presumed to apply in all instances.

Several different theories have been proposed to explain the phenomenon of heterosis. They are not completely exclusive of each other and so more than one mechanism may be involved in a particular case of heterosis (Shull, 1948).

Bruce (1910) assumed that dominance was positively correlated to vigor and showed mathematically that crossing two different breeds resulted in the decrease in the number of homozygous recessive genotypes. Therefore, a mean vigor greater than the collective mean vigor is produced. Inbreeding a Mendelian population reduces the mean number of homozygous and heterozygous dominants and so reduces vigor.

Keeble and Pellew (1910) similarly explained the greater height in certain of their pea hybrids by the accumulation of dominant growth factors in the zygote, some contributed by one parent and others by the other parent.

The assumption of a dominance hypothesis is that dominant genes are favorable while the recessive counterparts are deleterious. East and Jones (1919) maintained that natural selection eliminates

unfavorable dominant variations while unfavorable recessive variations tend to be perpetuated in the heterozygous state.

Two objections to the dominance hypothesis explaining heterosis have been raised. 1) Recombination should result in the appearance of an F_2 indivdual homozygous for all dominant factors present in the F_1. Resultant progeny of self-fertilizing such an F_2 individual would all be uniform and as vigorous as the F_1. Such an individual has not been enountered. 2) If independent dominant factors are responsible for heterosis, the distribution of the F_2 characters would be skewed with the mode being above the mean. In fact, a symmetrical distribution is often obtained (Collins, 1921).

Jones (1917) believed that linkage had not been considered. Different factors are associated into linkage groups by means of distribution on chromosomes. Actions of different factors may produce the same effect. Although each variety possesses favorable as well as unfavorable characters, varieties differ in the power of development. F_1 hybrids of inbred strains of maize are quite normal and display increased vigor over parental vigor since factors lacking in one are contributed by the other and vice versa. Because of linkage, different factors exist on different chromosomes and it is practically impossible for all dominants to be combined into the same chromosome. If the different factors are distributed on all the chromosomes, the individuals heterozygous for a certain number of factors would fall into classes following the expansion of the binomial $(a + b)^n$ which is an illustration of the normal frequency distribution.

Collins (1921) calculated that when 10 pairs of characters are involved, more than 100,000 individuals would be needed for the laws of probability to favor the appearance of one individual homozygous for all characters. Also, as the number of characters increases, the skewness of the distribution is not as marked. Collins also calculated that in consideration of twenty characters, 1,099,514,627,776 individuals were needed to compose a representative population of 21 classes in which 99.9% of the individuals fall into the 12 classes having the greatest number of dominants. A population of 500 individuals would greatly resemble the normal distribution.

Collins (1921) criticized Jones' linkage modification of the dominance theory as being "superfluous" in accounting for heterosis. Not dismissing the probability of linkage, he argued that the objections to the dominance theory that Jones' linkage theory refuted actually had no basis in fact.

Crow (1948) claimed that the dominance hypothesis could account for little of the increased vigor of hybrids. If vigor is evaluated in terms of selective advantage, its value would merely increase by 5% when all homozygous recessive factors are replaced.

Shull (1914) credited heterosis to the "dissimilarity in the gametes" forming the organism. This heterogeneity and unbalance of differences in the germ cells result in the stimulus to increased cell division, growth, etc. Within limits the more numerous the differences between gametes, the greater is the amount of stimulation. East and Hayes (1912) also arrived at the same hypothesis. The stimulus to development is increased by the heterozygous condition. The nature of

such a stimulus may be mechanical, chemical, or electrical. By this hypothesis, inbreeding itself is not a degenerative process but instead one of Mendelian segregation (East and Jones, 1919). Unfavorable recessives hidden in the heterozygous condition are isolated in the homozygous state. A decreased power of development is due to the lack of stimulation from heterozygosity.

East (1936) confirmed that heterosis increases as the genetic differences between parental stocks increase. Hybrids between pedigreed inbred stocks display increasing heterosis as the degree of relationship increases. Increased heterosis is also apparent when heterogamous stock is successively selfed prior to being crossed.

A. F. Shull (1912) criticized Shull's hypothesis since in accordance with this view, successive generations of inbreeding could produce a pure homozygous individual and every pure line must then reach its minimum in vigor which would be identical for all pure lines. Also, inbreeding must then always eventually reduce vigor provided random segregation and recombination occurred.

East (1910) proposed the possibility of several independently inherited allelomorphic pairs being involved in determining a particular character. The presence or absence of the dominant factor in these allelomorphic pairs would result in differing combinations, some producing the same effect on the character. The additive effects of presence or absence of the dominant factor results in quantitative variation. Hence, for a particular quantitative character, a number of genotypes may be responsible for the same expression.

East's example was based on the hypothesis of three allelomorphic pairs determining the number of rows on ears of maize. The basal unit is eight rows, the homozygous dominant condition of each locus contributes four rows, while the heterozygous state at each locus adds two rows. Therefore, the genotype AABBCC results in 20-rowed ears; AaBBCC, AABbCC, and AABBCc result in 18-rowed ears, etc. Since the same quantitative character may be due to differing genotypes, plants of 16-rowed ears may sometimes be obtained when crossing two plants having 12-rowed ears.

Hull (1945) assumed hybrid vigor to be a result of gene interaction. Assigning a value of 0.0 for the genotype aa and 1.0 for AA, a heterozygote with a value of 0.5 is intermediate between both parents and the locus does not contribute to hybrid vigor. As the heterozygote value approaches or exceeds 1.0, the importance of the locus in hybrid vigor is increased. Loci at which the heterozygote is superior to either homozygote contributes to hybrid vigor. The evidence of heterozygote values exceeding 1.0 is in the F_1 hybrids whose yields are in excess of the sum of the yields of two homozygous parents.

A. F. Shull (1912) recognized vigor to have its basis in metabolism. He hypothesized that when new nuclear elements encounter a cytoplasm in equilibrium as in cross-fertilization, the resulting interaction increases metabolism and hence vigor is observed. It is not the heterozygous condition in itself, but the interaction of the heterozygous nucleus (Mm) with the cytoplasm heretofore in equilibrium with an MM or mm nucleus that produces vigor. The effect of

the changed nucleus on the surrounding cytoplasm produces the stimulus to increased cell division. Here, Shull refuted East and Hayes' stance that the more rapid cell division determining vigor was stimulated by the heterozygous condition.

Jones (1945) observed recessive variations in inbred lines of maize which reduced growth but were not lethal. These variations he believed to be degenerative changes due to single allelic modifications. Upon crossing such mutant lines to the corresponding original inbred lines, a great amount of heterosis resulted. Heterosis, according to Jones, is "an accumulative effect of favorable heredity from both parents" even when involving single allelic differences (assuming multiple effects of genes).

Castle (1946) elaborated upon Jones' evidence. He proposed a sensitization by a new dominant allele A, appearing in the unorganized chromatin, on the chromatin at the opposite locus, resulting in a recessive allele a. This sensitization is in a manner like anaphylaxis. The two alleles establish two homozygous strains, AA in the mother strain and aa in the mutant daughter strain. Crossing these two strains differing in a single gene pair produces a hybrid with increased growth energy. In cases where hybrid vigor is not apparent when two inbred lines are crossed, the sensitized recessive allele a is absent.

Heterozygosity of the single gene pair Mama, concerning photoperiodic response and time of floral initiation in sorghum, was found to produce heterosis comparable in degree to commercial maize hybrids. Quinby and Karper (1946) thus interpreted their data as supporting

the theory of interaction between unlike allelomorphs as the plausible explanation of heterosis. The stimulation to tillering and cell division derived from this heterozygous condition was also believed to be due to an increased capacity to utilize the available nutrient supply.

The genes determining physiological efficiency are much greater in number than genes determining morphological characters. Heterosis is mainly concerned with the speed of physiological reactions. Genes may be classified into two types--those that cause breakdowns in physiological processes and those that do not. A defective gene may be compensated for by a normal allele in the pair, and the respective processes are usually not affected. The heterosis observed when two long-inbred lines are crossed involved the "different genic isomers of the physiologically active and more or less normal genes." Non-defective intra-allelic genes, each diverging from each other in function, may have additive effects. Heterozygotes become more efficient as the component alleles diverge more greatly (East, 1936).

Homozygous strains of Drosophila melanogaster exhibit greater variance within a strain than do heterozygous strains. Decline due to inbreeding is apparent in the character of size, and heterosis is manifested in increased size and vigor as well as reduced susceptibility to environmental fluctuations. Robertson and Reeve (1952) theorized that a greater degree of heterozygosity means a greater diversity of alleles which provide "greater biochemical versatility in development." Heterosis is exhibited because of the superior ability of a highly heterozygous individual to efficiently use the available

nutrients and the decrease in susceptibility to environmental fluctuations since more alternatives of overcoming such obstacles to development are available.

East (1936) emphasized that heterosis effects cannot be compared among different genera. Genetic evidence points to greater variation in some genera than others--mutation rates being higher in some. Hence, each genus requires individual consideration.

MacKey (1976) pointed out that heterozygosity in itself does not bestow heterosis nor does homozygosity per se exclude heterosis. The modern concept of heterosis was subdivided into three categories: direction, function, and transmissibility through sexual phase. Direction of heterosis may be positive or negative--positive when parental values are exceeded and negative when inferior to parental values. Heterosis may be interpreted in terms of function--luxuriance (exhibition of vigor in yield, plant size, etc.), adaptive capabilities of the plant, selective advantage or reproductive ability. The transmissibility of heterosis to the next sexual generation may be unfixable due to free segregation of the heterozygosity or fixable in a balanced heterozygous or homozygous composition. Heterosis may be viewed in an individual in conflicting ways--a luxuriant plant with adaptive advantages may have no reproductive ability. Therefore, there is no standard method of measuring heterosis.

Different mechanisms of heterosis have been proposed and all probably play some part in this complex phenomenon. MacKey (1976) subdivided regulatory systems of heterosis into: genomic (nonallelic or allelic heterosis), plasmatic heterosis or nonheritable heterosis.

Nonallelic heterosis includes transgressive (additive, cumulative), recombinative (complementary) and epistatic heterosis. Allelic heterosis involves dominant or overdominant heterosis.

In agricultural crops, heterosis expressed in yield is often analyzed. Hayes and Foster (1976) generalized that in most of the studies done on self-pollinating crops, grain yield inheritance appears complex; dominance and epistasis, and sometimes overdominance are strongly indicated. The best F_1 hybrids would result from crossing parents with a high proportion of additive, dominant or complementary epistatic genes for the desired character expression of the main components of yield. In maize, Robinson and Cockerham (1961) found heterozygosity to be linearly related to yield and ear height. After selecting for both high and low combining ability with an inbred line, Penny et al. (1962) concluded that their selection in maize was for genes having complete or partial dominance or mainly additive effects. Epistasis was suggested by Gorsline (1961) to be involved in the characters of yield, grain moisture, silking, stalk quality, plant height, ear node height, percent ear node height, ear length, ear diameter, and ear length/diameter ratio in maize hybrids; epistasis by environment interactions were also found to be significant and common.

Schwartz (1960) first established the presence of hybrid enzymes in maize with the E_1 esterase. Schwartz and Laughner (1969) found the Adh_1F allele in maize to code for an active but labile dimer (FF) and the Adh_1Cm allele to specify a less active but more stable enzyme (CmCm); the heterodimer (FCm) was formed in the heterozygote which was

both active and stable. Therefore, since activity and stability of an enzyme enhance growth and development of an organism, such hybrid enzymes were proposed as being, in part, responsible for hybrid vigor.

McDaniel and Sarkissian (1966) found a heterototic maize hybrid to possess mitochondrial activity not different from that of a mixture of parental mitochondria; hence, mitochondrial complementation was proposed as an aspect of heterosis. Mitochondrial polymorphism was later found to exist in maize; the hybrid possessed parental types of mitochondria as well as an intermediate type which contributed about 30% of the cytochrome c oxidase activity (Sarkissian and McDaniel, 1967). Mitochondrial heterosis in maize was found to involve superior coupling of the NAD-linked mitochondrial enzymes, thus enabling more efficient electron transport and oxidative phosphorylation to promote superior growth of the hybrid (McDaniel and Sarkissian, 1968). Mitochondria of a wheat hybrid surpassed parental mitochondria in ADP:O ratios and in respiratory control when utilizing alpha-ketoglutarate, malate and succinate; highest ATPase activity was observed in the hybrid mitochondria--growth of a heterotic organism would be enhanced by the availability of ATP (Sarkissian and Srivastava, 1969).

Maternal influence in plants, such as seed maturation, seed size, endosperm character, seed dormancy, etc., may be critical influences upon the hybrid offspring and its relative vigor (MacKey, 1976).

An observed phenomenon has been that after a number of generations of maintining the inbred lines, the hybrid population decreases or completely loses the heterotic effect originally

possessed and detrimental characters sometimes appear. Applying population-genetic theory to this problem, Svab (1976) explained that often parental lines are maintained with a small number of individuals, only one being the extreme. Therefore, with such a small sample size, random drift operates. A mutant gene, chromosomal mutation or partially preserved heterozygosity may be incorporated into the line maintained. Such genetic changes in the inbred lines may then influence the dominance and epistatic conditions and consequently, the final heterotic effect.

Heterosis of a character can be seen as resulting from a genetic balance of "differently directed factors." Since expression of heterosis is seen in separate characters or a complex of characters, rather than in the total plant organization, sources of heterosis can be concluded to be formed and located in separate genetic systems of the hybrid (Konarev, 1976).

Cross- and self-fertilization in orchids

The floral structures of many species of Orchidaceae were examined by Darwin (1904). He was impressed by the multitude of devices and variety in structure, all ensuring the common end of cross-fertilization. Some species of orchids are primarily or frequently self-fertilized, yet retain various structures adapted for cross-fertilization despite the fact that they are rarely, if ever, involved. Darwin thus concluded that such species were descended from plants cross-fertilized by insects. Under conditions of limited or no insect visitation, floral structure was gradually modified to allow

for self-fertilization. Self-fertilized seeds are more advantageous to the perpetuation of the species than very few or no seeds.

Since orchid pollen must be required in a large amount to produce the great quantity of seed found in orchids and is located in anthers just above or behind the stigma, it would more safely and easily be utilized in self-fertilization than in cross-pollination where transport is necessary. Darwin, noting the beneficial effects in most cases of cross-fertilization in orchids, felt that this demonstrated that Nature "abhors perpetual self-fertilization."

Amphidiploidy

Constant species hybrids have been reported since the 1880s (Goodspeed and Bradley, 1942). Through cytological investigation, Skovsted (1929) showed that Aesculus carnea Willd., a morphologically and cytologically constant species, arose by the crossing of species with subsequent chromosome doubling. A fertile F_1 plant of a cross between Nicotiana glutinosa and Nicotiana tabacum was found to have twice the chromosome number of other similar sterile F_1 plants, the doubling believed to have occurred immediately or soon after fertilization (Clausen and Goodspeed, 1925). Artificial crossing of Brassica napus L. and Brassica campestris L. resulted in a normal diploid F_1 plant, the F_2 progeny of which were amphidiploid probably due to somatic doubling of the zygote (Frandsen and Winge, 1932). A cross of diploid Fragaria bracteata and a diploid Fragaria Helleri produced a tetraploid plant, whose F_2 progeny was uniform and

morphologically distinct, thus being regarded as a new species (Ichijima, 1926).

Amphidiploids may originate from fusion of diploid gametes from different autopolypoid sources. In F_1 meiotic divisions, a diploid gamete may arise from non-conjunction of chromosomes and inadequate formation of the spindle, whereby the chromosomes fail to move to opposite poles. Thus, one nucleus is formed and after the second meiotic division, two nuclei with the full somatic complement of the hybrid are produced (Goodspeed and Bradley, 1942). Non-reduction may occur at the first meiotic division. The bivalents separate and each chromosome is positioned at the equator; no first division occurs. Each chromosome splits lengthwise and 2n separate chromosomes pass to each pole (Belling, 1925). Belling (1925) used the term non-division for failure of the second meiotic division; diploid gametes may also result. Sometimes, in cells of the archesporium, just prior to reduction division, the chromosomes split without the occurrence of cell division. Meiosis proceeds with conjugation of homologous chromosomes and diploid gametes are produced (Karpechenko, 1927). Non-reduction in one type of gamete, male or female, for two successive generations along with backcrossing can lead to amphidiploidy (Goodspeed and Bradley, 1942).

Fusion of homotypic spindles during meiosis was observed in pollen mother cells of a Galeopsis pubescens X Galeopsis speciosa hybrid; this was believed to lead to the formation of an unreduced gamete (Muntzing, 1930).

Three mechanisms where 2n gametes are produced have been observed in pollen formation of diploid potatoes. Parallel spindles in the second meiotic division, instead of the normal 60 degree angle producing microspores in a tetrahedron, result in a dyad of 2n microspores. Premature cytokinesis 1 involves asynchronized and irregular movement of the chromosomes at metaphase I and anaphase I; at telophase I, the chromatids fall apart and a cleavage takes place. No second division occurs and again a dyad of two 2n microspores is produced. Premature cytokinesis 2 has a normal first meiotic division, cytokinesis occurs at prophase II, and there is no second division--a dyad of 2n microspores results. Genetically, these diploid gametes originating through the parallel spindles mechanism can be thought to be first division restitution gametes; all heterozygous loci from the centromere to the first crossover will remain heterozygous as well as one-half of the heterozygous loci between the first and the second crossover. Premature cytokinesis 1 and 2 produce 2n gametes genetically equivalent to second division restitution gametes where all heterozygous loci from the centromere to the first crossover in the parent will be homozygous while the heterozygous loci between the first and the second crossover will be heterozygous (Mok and Peloquin, 1975).

Somatic doubling of the chromosome complement of an F_1 hybrid produces amphidiploidy (Goodspeed and Bradley, 1942). As previously mentioned, chromosome doubling in the zygote was thought to account for the amphidiploid forms of Nicotiana glutinosa X Nicotiana tabacum (Clausen and Goodspeed, 1925) and Brassica napus X Brassica campestris

(Frandsen and Winge, 1932). Somatic doubling in the meristem of a lateral bud resulted in a tetraploid fertile stem arising on a diploid hybrid of Primula floribunda X Primula verticillata (Newton and Pellew, 1929). Parthenogenetic origin of an amphidiploid of the F_1 hybrid of Nicotiana glauca and Nicotiana Langsdorffii was believed to be from a monad (Kostoff, 1938).

A remote source of amphidiploidy is the hybridization of two autotetraploid plants. Multivalent formation in meiosis of autotetraploids leads to many polysomic and deficient gametes with low viability. Thus, perfect amphidiploids may not be formed from tetraploid hybridization due to a chromosomally aberrant nature (Goodspeed and Bradley, 1942).

Chromosome conjugation in amphidiploids is of two types--autosyndesis and allosyndesis. Autosyndesis involves conjugation of chromosomes descended from the same species or subspecies while allosyndesis involves conjugation of chromosomes descended from different species or subspecies. Chromosome conjugation indicates some structural similarity in gene arrangement between these chromosomes (Goodspeed and Bradley, 1942). However, chromosome pairing can be disrupted by gene mutations which can disturb any stage of meiosis (Dobzhansky, 1941).

Clear-cut distinction between autosyndesis and allosyndesis is not always possible since allopolyploids display a gradation in pairing behavior from slight to great differentiation between homologues derived from different parents (Darlington, 1932). The F_1 hybrid of Crepis rubra and Crepis foetida shows complete pairing of

homologous chromosomes and quadrivalent formation is frequent in the amphidiploid, thus indicating a close relationship between the parent species (Poole, 1931). Nine loosely paired bivalents are observed in the F_1 hybrid Primula kewensis (Primula floribunda X Primula verticillata), while in the amphidiploids one quadrivalent and 16 bivalents frequently occur (Newton and Pellew, 1929). No chromosome conjugation is observed in the F_1 hybrid of Raphanus sativa and Brassica oleracea but the amphidiploid displays complete conjugation, homologous cabbage chromosomes forming bivalents and homologous radish chromosomes pairing (Karpechenko, 1927). Such pairing, where no allosyndesis occurs, indicates the two parental forms to be true, legitimate, genetic species (Lindstrom, 1936). In amphidiploids of distantly related species or of intergeneric crosses, autosyndesis is generally the rule (almost complete lack of pairing occurring in the original diploid F_1 hybrid) (Goodspeed and Bradley, 1942). Cytological and genetic evidence showed that unlike chromosomes (from different species) in the amphidiploid of Lycopersicon esculentum and Lycopersicon pimpinellifolium paired (Lindstrom and Humphrey, 1933). Chromosome pairing can occur at random, as shown by flower color segregation in the amphidiploid of Fragaria (Yarnell, 1931). Differential affinity of dissimilar chromosomes in the presence or absence of identical partners can be viewed in terms of "pairing blocks"; similar portions of chromosomes which can pair may be distributed in different segments of dissimilar chromosomes, determining the conjugation behavior (Darlington, 1932). Random assortment of eight chromatids can occur when four chromosomes are

associated at prophase; crossing-over between the eight chromatids would approach a random interchange (Lindstrom, 1936).

CHAPTER I

INBREEDING AND SELECTION IN AMPHIDIPLOID D. JAQUELYN THOMAS

1.1 Materials and Methods

The cross between Dendrobium gouldii and D. phalaenopsis is given the hybrid name, D. Jaquelyn Thomas. A cross of a diploid white D. gouldii and a diploid D. phalaenopsis 'Lyon's Light No. 1' (white with pinkish tinge on the abaxial petal and sepal surfaces) produced primarily diploid offspring, with the exception of one tetraploid plant (labeled Y166-1). Diploid D. Jaquelyn Thomas plants, when selfed, can be infertile (Kamemoto et al., 1964). The tetraploid, with twice the number of chromosomes as the diploid, was selfed and was fertile. The flowers of the S_1 (first selfed generation) progeny were similar to those of the parent and were relatively uniform. Such breeding behavior of D. Jaquelyn Thomas 'Y166-1' implied that it is an amphidiploid with two chromosome sets from D. gouldii and two from D. phalaenopsis.

Selfing the amphidiploid parent plant 'Y166-1' produced an S_1 generation from which two individuals (UH44-5 and UH44-50) were selected (Fig. 1). Y166-1 has relatively small flowers with a conspicuous pink tinge. UH44-50 was selected because of its comparatively larger and whiter flowers (Fig. 2). UH44-5, on the other hand, was picked at random and has smaller and more darkly tinged flowers than Y166-1. Selfing UH44-50 produced the S_2 (second selfed) generation from which K159-19 and K159-21 were selected for their large flower size and whiter color (Fig. 1). A tetraploid plant

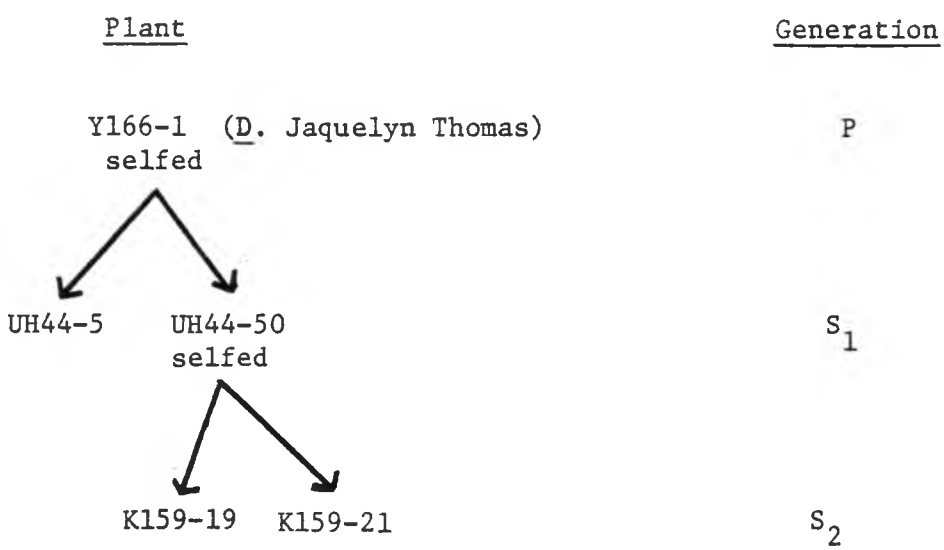

Figure 1. Relationships of D. Jaquelyn Thomas plants involved in the inbred matings.

Figure 2. Flowers of the S_1 progeny (D. Jaquelyn Thomas 'Y166-1' selfed). UH44-50 was selected for its large flower size and light pink tinge.

(2097-4N) was obtained from a diploid D. Neo Hawaii hybrid (D. phalaenopsis X D. gouldii) in tissue culture. This D. Neo Hawaii plant, with greenish-white flowers, is believed to be an amphidiploid arising from somatic doubling.

One noninbred and nine inbred matings were studied. Table 1 details these matings. The parent amphidiploid Y166-1, the randomly picked UH44-5 (S_1) and the selected K159-19 (S_2) were selfed. The S_1 plants UH44-50 and UH44-5 were sibmated as were the S_2 plants K159-19 and K159-21 (in reciprocal crosses). UH44-50, the selected S_1 plant, was backcrossed to the parent Y166-1; reciprocal backcrosses of the selected S_2 plant K159-21 to Y166-1 were also made. The noninbred cross of K159 to D. Neo Hawaii '2097-4N' was included.

Pollinations were done on November 1 or 3, 1972. About two and one half months later, on January 16, 1973, the pods were harvested and the seeds were aseptically sown on modified Vacin and Went medium for germination (Table 23). On April 17, 1973, three months later, about 100-150 randomly picked seedlings were transflasked to 500 ml flasks of modified Vacin and Went medium for transflasking (Table 24). Approximately 70 of the larger seedlings in each flask were transferred to a community pot about seven months later on October 9, 1973. Thirty-two of the larger plants from each community pot were individually potted into 2-inch clay pots on May 29, 1974, seven and a half months later. On March 3, 1975, nine months later, the twenty most vigorous plants from each progeny were potted into 6-inch cement

Table 1. Inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated
P selfed (S_1)	1	Y166-1 selfed
S_1 selfed (S_2)	3	UH44-5 selfed
S_2 selfed (S_3)	6	K159-19 selfed
S_1 sibmated	4	UH44-50 sibmated to UH44-5
S_2 sibmated	7	K159-19 sibmated to K159-21
S_2 sibmated	8	K159-21 sibmated to K159-19
S_1 X P (BC_1)	5	UH44-50 X Y166-1
P X S_2 (BC_2)	2	Y166-1 X K159-21
S_2 X P (BC_2)	9	K159-21 X Y166-1
Noninbred cross	10	2097-4N X K159-21

pots and placed in the orchid saran house at the Upper Manoa Campus of the University of Hawaii.

A randomized complete block statistical design was used. The twenty plants of each progeny were ranked from 1 to 20 in decreasing order of size. Individuals of the same rank from different progenies formed a block. The blocks were randomly assigned positions on two benches; within each block, plants of the different progenies were also randomly arranged. Guard rows were placed at both ends of the benches. When increasing plant growth necessitated greater spacing, half of the pots on each bench were transferred, in a serpentine sequence, to the adjacent bench. The remaining pots were also rearranged in a serpentine sequence. Thus, blocks were kept intact. Guard rows were again used at the ends of the benches.

In August, 1975, the first plant flowered. Flowering of the other plants followed in time. Flowers were harvested and floral data were taken until the end of December, 1978. Flower racemes were harvested when 75-80% of the flower buds on the raceme were open. Harvesting was done almost daily during times of high productivity, and done at longer intervals at other times of the year. Racemes were harvested in the morning to reduce the effects of the day's heat on vase life. Scape length, the distance from the stem base to the lowest initiated flower, was measured on the plant prior to harvest.

Yield was expressed as the number of harvested racemes having ten or more initiated flowers; racemes having fewer than 10 initiated flower buds were discarded since they are unsalable. Since all of the plants were of the same age and yield data were taken for the same

period of time, the earliness of the beginning of flowering was one factor contributing to the total count of racemes from a plant--this may have caused one plant to yield more racemes during this period than another. However, this earlier flowering may be construed as a component of vigor by the farmer.

Shortly after harvest, flower racemes were immersed in water for 15 minutes and then transferred to 500 ml flasks of tap water. Several measurements were subsequently made. Raceme length was calculated as the scape length plus the stem measurement from the lowest initiated flower to the tip of the raceme. Flower size was taken as the broadest measurement across the third lowest flower on the raceme. Color of the flowers on a raceme was rated as 1 (light pink tinge), 2 (moderate pink tinge), or 3 (heavy pink tinge) (Fig. 3). The total number of initiated flowers was determined by adding the number of flowers and buds on the raceme at harvest and the number of buds which had dropped prior to harvest. The percentage of bud drop per raceme was calculated by dividing the number of buds which had dropped before harvest by the total number of initiated flowers.

The flowers were set in an air-conditioned laboratory where an approximate temperature of 23 degrees C. and a humidity level of 50% were normally maintained. No more than 4 racemes were initially apportioned to a flask, and never were surviving racemes from different flasks consolidated into one. Water in the flask was changed three times a week, at which time any slime on the scape was rinsed off and the basal part of the stem snipped back. Vase life

Figure 3. Ranking of flower color: 1 (light tinge), 2 (moderate tinge) and 3 (heavy tinge).

was interpreted as the half life of the raceme--the number of days the raceme lasted until half of the flowers present at harvest either senesced or wilted.

Growth of the dendrobium plant is sympodial. During early growth, successive shoots are increasingly taller. However, larger shoots can be shorter than older shoots. During the period of early growth when shoot heights were low and unsynchronized, it was difficult to obtain meaningful data. Hence, height data were taken at the termination of the experiment. Plant height, from the base of the shoot to the "V" of the uppermost leaves was measured to obtain the maximum height of the plant. Secondly, the most recently matured shoot was measured to assess height differences after the plant had completed a period of heavy raceme production--many of these shoots were shorter than the tallest shoot of the plant.

Data for individual plants were obtained for total yield (number of racemes harvested) (Tables 25 to 29) and shoot height (Tables 30 and 31); mean values for flower size, flower color, scape length, raceme length, number of initiated flowers per raceme, vase life and percent bud drop were found for each individual (Tables 32 to 38). Analyses of variance were performed on these values (except flower color) (Tables 39 to 42). Broken shoots or orchid weevil damage on several plants resulted in missing data for height of the most recently matured shoot. Therefore, one replicate with 3 missing measurements was omitted from the analysis while 5 replicates, each with a single missing measurement had these values estimated prior to

analysis. Comparisons among the means of progenies for each character were done using Duncan's Bayesian least significant difference test (Duncan, 1965).

Bench effects were analyzed as a completely randomized design. For each character analyzed, benches were the treatments (Table 43). Total yield, height of the tallest shoot, flower size, scape length, raceme length, number of initiated flowers per raceme, vase life and percent bud drop were the characters analyzed by bench.

The parental plants used in selfings and crossings were of different ages and in different states of vitality. Because these parental plants could not be directly compared with each other, data on the parental plants were used as references in interpreting data on certain characters. Floral and height data were taken in the same way as done on the experimental plants.

1.2 Results and Discussion

Flower size and color

The largest flowers were obtained in progenies 6, 7 and 8. The S_2 progeny (progeny 3) was the result of selfing a randomly chosen S_1 individual (UH44-5), whose flower size was smaller than UH44-50 (Table 2); flower size of progeny 3 was smallest of all progenies (Table 2). Progeny of a backcross of UH44-50 to Y166-1 did not differ in flower size from that of Y166-1 selfed (S_1) (Table 2). Selected K59-21 (large-flowered), when backcrossed to Y166-1, generated offspring with flower size intermediate to that possessed by progeny of Y166-1 selfed (S_1) and K159-91 selfed (S_3). The noninbred progeny (progeny 10) had a mean flower size just smaller than that of progenies 6, 7 and 8.

Since a normal distribution was not evident from the data on flower color (Table 33), analysis of variance could not be performed. In certain progenies, flower color ranking of all replicates varied little from 1.0 or 3.0. Backcrosses of S_2 plants to the parent (progenies 2 and 9) showed clustering around a 2 ranking, while the sibmating in the S_1 (progeny 4) and the backcross of an S_1 plant to the parent (progeny 5) showed a range spanning from a 1.8 or 2.0 to 3.0. Although the flower color was given an absolute rank of 1, 2, or 3, a distribution was observed. The pink tinge appeared in a range and an absolute rank had to be attached to it for the lack of another method of data-taking.

Table 2. Progeny means of flower size in inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Flower Size (mm)
P selfed (S_1)	1	Y166-1 selfed	57.3 d[z]
S_1 selfed (S_2)	3	UH44-5[y] selfed	52.4 f
S_2 selfed (S_3)	6	K159-19[x] selfed	66.1 a
S_1 sibmated	4	UH44-50 X UH44-5	55.0 e
S_2 sibmated	7	K159-19 X K159-21	67.3 a
S_2 sibmated	8	K159-21 X K159-19	67.1 a
S_1 X P (BC_1)	5	UH44-50 X Y166-1	58.0 d
P X S_2 (BC_2)	2	Y166-1 X K159-21	60.6 c
S_2 X P (BC_2)	9	K159-21 X Y166-1	60.7 c
Noninbred cross	10	2097-4N X K159-21	62.6 b

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least significant difference for multiple-comparison testing.

[y]UH44 is the progeny of Y166-1 selfed.

[x]K159 is the progeny of UH44-50 selfed.

The most selected progenies (progenies 6, 7 and 8) displayed the least amount of pink tinge (Table 3); parent plants which were selected for their light tinge were K159-19 and K159-21 (Table 4). Progenies of Y166-1 selfed (progeny 1) and randomly selected UH44-5 selfed (progeny 3) showed the greatest amount of tinge. Crossing an individual selected for light tinge (UH44-50 or K159-21) with an individual that was not (Y166-1 or UH44-5) resulted in progenies (progenies 2, 4, 5 and 9) whose degree of tinge showed a range between the two parents. The noninbred progeny, having 2097-4N with greenish-white flowers as one of its parents, showed little pink tinge.

Larger flowers with lighter pink tinge resulted from the selection. Figure 2 shows the range in the S_1 progeny from which UH44-50 was selected for large flower size and light pink tinge. Flower measurement of several racemes show the difference in flower width and degree of tinge of selected UH44-50 and randomly chosen UH44-5 (Table 4). Selfing of UH44-50 produced K159-19 and K159-21, both selected for large size and light tinge (Table 4). Since S_2 progeny from UH44-50 was not included in this study, a progression in flower size increase and lightening of the pink tinge, visually seen in Figure 4, is not seen in Table 3. However, progenies of the S_3 (progeny 6) and the S_2 sibmatings (progenies 7 and 8), all derived from UH44-50, were larger and lighter-tinged than the original parent Y166-1 and the progeny 1 (derived from selfing Y166-1) (Tables 2, 3 and 4).

Figure 2 shows some of the variation existing in the S_2 generation (Y166-1 selfed). This variation, evidenced by slight

Table 3. Progeny means of flower color ranking in inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Flower Color Ranking
P selfed (S_1)	1	Y166-1 selfed	2.97
S_1 selfed (S_2)	3	UH44-5[z] selfed	2.90
S_2 selfed (S_3)	6	K159-19[y] selfed	1.01
S_1 sibmated	4	UH44-50 X UH44-5	2.44
S_2 sibmated	7	K159-19 X K159-21	1.03
S_2 sibmated	8	K159-21 X K159-19	1.01
S_1 X P (BC_1)	5	UH44-50 X Y166-1	2.55
P X S_2 (BC_2)	2	Y166-1 X K159-21	2.00
S_2 X P (BC_2)	9	K159-21 X Y166-1	2.07
Noninbred cross	10	2097-4N X K159-21	1.02

[z]UH44 is the progeny of Y166-1 selfed.

[y]K159 is the progeny of UH44-50 selfed.

Table 4. Mean character values of amphidiploid D. Jaquelym Thomas and amphidiploid D. Neo Hawaii.

Parent	Generation	Number of Racemes Evaluated	Flower Size (mm)	Color Ranking	Scape Length (cm)	Raceme Length	Total Flowers	Vase Life (Days)	Percent Bud Drop
Y166-1	P	30	57.6	2.9	17.8	61.0	20.2	10.1	2.0
UH44-5	S_1	5	45.0	2.8	19.8	51.2	16.2	9.6	7.9
UH44-50	S_1	7	54.3	1.7	17.2	42.7	14.4	13.6	0.0
K159-19	S_2	25	63.8	1.0	17.6	57.2	17.3	9.4	2.1
K159-21	S_2	13	61.8	1.0	18.2	51.3	16.5	11.3	0.0
2097-4N	P	2	61.5	no tinge	19.8	54.5	15.5	--	--

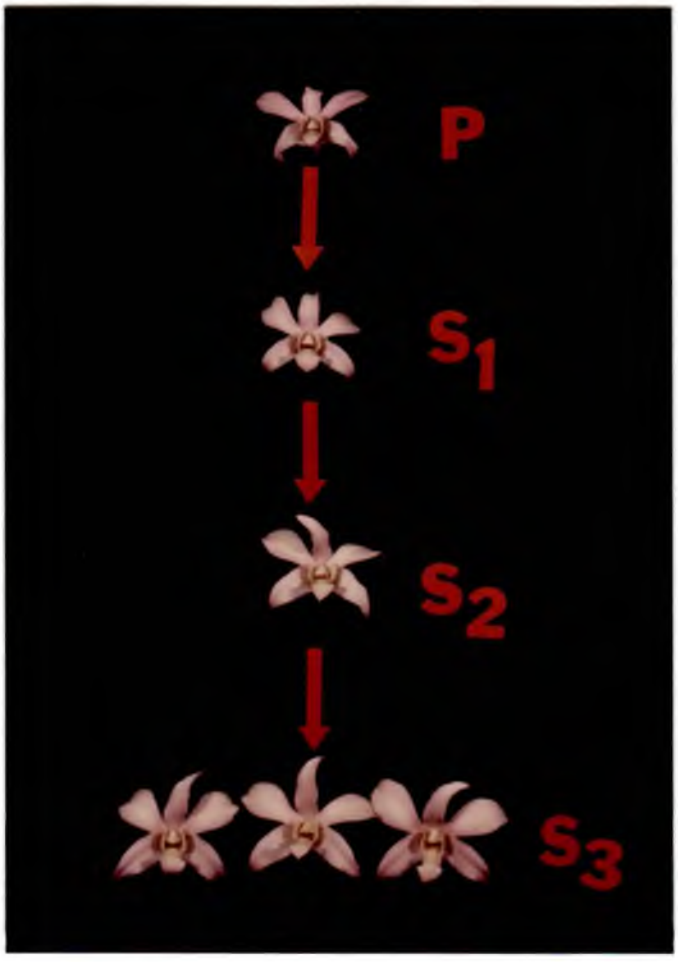

Figure 4. Visual impression of the increase in flower size and color purity from the parent Y166-1 to the selected S_1 plant (UH44-50) to the S_2 (K159 progeny) to the S_3 (progeny 6).

flower differences, is due to genetic differences. The amphidiploid Y166-1 may have originated from either the union of two unreduced gametes or from somatic doubling. Heterozygosity within the genomes may be responsible for the variation if unreduced gametes formed the zygote. If one or both of the gametes were the result of first division restitution, heterozygosity can be retained in homologous chromosomes of the same genome. Another possibility for the variation, in the case of unreduced gametes forming the zygote or of somatic doubling, is allosyndesis (conjugation of chromosomes descended from different species). Kamemoto et al. (1964) found normal meiosis with 38 bivalents and normal tetrads of microspores in a different (not Y166-1) tetraploid D. Jaquelyn Thomas hybrid. Hence, autosyndesis (conjugation of chromosomes of the same species) commonly occurs in the amphidiploid. The production of normal tetrads indicates that the distribution of chromosomes to the poles is regular and the chromosome sets of each diploid parent species migrate to each pole. Thus, the resulting amphidiploid progeny from selfing can be expected to be uniform. However, since diploid (2n=38) D. Jaquelyn Thomas hybrids have been found to form 19-13 bivalents in meiosis (Kamemoto et al., 1964), it is also possible that occasionally allosyndesis could occur, causing some minor variation in the progeny. Crossing-over in allosyndesis could also increase the genetic variation in the resulting gametes. Y166-1 does produce minor variations in its progeny which allows the opportunity for selection of desired characteristics.

Selection for an extreme variant in terms of flower size and color was made in the selfed progeny of the amphidiploid Y166-1. This variant was selfed, and further selection and selfing resulted in offspring of a genetic constitution characterized by large, white flowers with only a slight pink tinge. Therefore, this method involving selection and selfing was successful in increasing the flower size and decreasing the amount of pink tinge in the flowers of inbred progenies derived from D. Jaquelyn Thomas 'Y166-1'.

By inbreeding, the genetic segregation process produced a range of genotypes, varying in the proportion of homozygous loci. Selection for the two characters of large flower size and purer flower color, with subsequent selfing, selection and further selfing, probably isolated a genetic constitution fairly homozygous for the flower size and low pink tinge characteristics, along with other linked genes. Generally, overall homozygosity in a population is increased with inbreeding; however, genotypes with a greater proportion of heterozygous loci exist. Therefore, selection for the most vigorous-appearing plants of the progeny may have caused the more heterozygous individuals to be retained.

Other floral characters

S_1 progeny (progeny 1) of Y166-1 selfed had the shortest mean scape length while the noninbred seedlings (progeny 10) had the longest mean scape length (Table 5). This reflects parental data (Table 4) where 2097-4N and K159-21 possessed long scapes in comparison to Y166-1. Like 2097-4N, UH44-5 had a relatively long

Table 5. Progeny means of scape length in inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Scape Length (cm)
P selfed (S_1)	1	Y166-1 selfed	17.0 e[z]
S_1 selfed (S_2)	3	UH44-5[y] selfed	19.3 b
S_2 selfed (S_3)	6	K159-19[x] selfed	19.0 bc
S_1 sibmated	4	UH44-50 X UH44-5	19.0 bc
S_2 sibmated	7	K159-19 X K159-21	18.4 cd
S_2 sibmated	8	K159-21 X K159-19	18.7 bcd
S_1 X P (BC_1)	5	UH44-50 X Y166-1	18.1 d
P X S_2 (BC_2)	2	Y166-1 X K159-21	18.1 d
S_2 X P (BC_2)	9	K159-21 X Y166-1	18.7 bcd
Noninbred cross	10	2097-4N X K159-21	21.6 a

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least significant difference for multiple comparison testing.

[y]UH44 is the progeny of Y166-1 selfed.

[x]K159 is the progeny of UH44-50 selfed.

scape length (Table 4) and its S_2 progeny (progeny 3) had the second longest scape. Other progenies ranged between these values.

Progeny 4 had the shortest raceme length (Table 6), but did not differ from progenies 1, 5, 6 and 9. Progenies 1, 2, 3, 5, 6, 7, 8, 9 and 10 did not differ from each other in total raceme length.

Progeny 1 produced the greatest number of initiated flowers per raceme, though not significantly more than progeny 2 (Table 7). The most inbred seedlings (progenies 6, 7 and 8) produced the fewest flowers per raceme, the next higher number of flowers per raceme being of the noninbred progeny (progeny 10). The progenies of the backcrosses to the parent Y166-1 (progenies 2, 5 and 9), the S_1 sibmating (progeny 4) and the S_2 (progeny 3) had still more initiated flowers per raceme, though less than the S_1 progeny.

Flower racemes from progenies of the noninbred cross (progeny 10), the S_2 (progeny 3) and the S_1 sibmating (progeny 4) lasted longest (Table 8). Vase lives of racemes from the other progenies were lower and overlapping in significance. Many environmental and handling factors are involved in vase life, and so due to the different growing conditions of some parental plants and the experimental plants (saran house vs. greenhouse) vase life of the parental plants and the progenies are not directly comparable.

Bud dropping occurred with low frequency in the progenies (Table 9). However, the individual UH44-5 did show a greater propensity than did the other parents (Table 4), and genetic basis for this was recognized when the offspring of selfing UH44-5 (progeny 3)

Table 6. Progeny means of raceme length in inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Raceme Length (cm)
P selfed (S_1)	1	Y166-1 selfed	63.5 ab[z]
S_1 selfed (S_2)	3	UH44-5[y] selfed	64.7 a
S_2 selfed (S_3)	6	K159-19[x] selfed	62.7 ab
S_1 sibmated	4	UH44-50 X UH44-5	64.5 a
S_2 sibmated	7	K159-19 X K159-21	60.6 b
S_2 sibmated	8	K159-21 X K159-19	63.0 ab
S_1 X P (BC_1)	5	UH44-50 X Y166-1	64.0 ab
P X S_2 (BC_2)	2	Y166-1 X K159-21	65.5 a
S_2 X P (BC_2)	9	K159-21 X Y166-1	64.5 a
Noninbred cross	10	2097-4N X K159-21	66.0 a

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least significant difference for multiple comparison testing.

[y]UH44 is the progeny of Y166-1 selfed.

[x]K159 is the progeny of UH44-50 selfed.

Table 7. Progeny means of number of initiated flowers per raceme in inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Number of Initiated Flowers Per Raceme
P selfed (S_1)	1	Y166-1 selfed	22.8 a[z]
S_1 selfed (S_2)	3	UH44-5[y] selfed	21.2 b
S_2 selfed (S_3)	6	K159-19[x] selfed	18.7 d
S_1 sibmated	4	UH44-50 X UH44-5	21.4 b
S_2 sibmated	7	K159-19 X K159-21	18.5 d
S_2 sibmated	8	K159-21 X K159-19	19.0 d
S_1 X P (BC_1)	5	UH44-50 X Y166-1	21.7 b
P X S_2 (BC_2)	2	Y166-1 X K159-21	22.0 ab
S_2 X P (BC_2)	9	K159-21 X Y166-1	21.5 b
Noninbred cross	10	2097-4N X K159-21	20.2 c

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least significant difference for multiple comparison testing.

[y]UH44 is the progeny of Y166-1 selfed.

[x]K159 is the progeny of UH44-50 selfed.

Table 8. Progeny means of vase life in inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Vase Life (Days)
P selfed (S_1)	1	Y166-1 selfed	11.5 b
S_1 selfed (S_2)	3	UH44-5[y] selfed	12.6 a
S_2 selfed (S_3)	6	K159-19[x] selfed	10.5 d
S_1 sibmated	4	UH44-50 X UH44-5	12.4 a
S_2 sibmated	7	K159-19 X K159-21	11.0 bcd
S_2 sibmated	8	K159-21 X K159-19	10.7 cd
S_1 X P (BC_1)	5	UH44-50 X Y166-1	11.5 b
P X S_2 (BC_2)	2	Y166-1 X K159-21	11.3 bc
S_2 X P (BC_2)	9	K159-21 X Y166-1	11.0 bcd
Noninbred cross	10	2097-4N X K159-21	12.7 a

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least significant difference for multiple comparison testing.

[y]UH44 is the progeny of Y166-1 selfed.

[x]K159 is the progeny of UH44-50 selfed.

Table 9. Progeny means of percent bud drop per raceme in inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Percent Bud Drop Per Raceme
P selfed (S_1)	1	Y166-1 selfed	2.0 c[z]
S_1 selfed (S_2)	3	UH44-5[y] selfed	5.8 a
S_2 selfed (S_3)	6	K159-19[x] selfed	1.8 c
S_1 sibmated	4	UH44-50 X UH44-5	4.0 b
S_2 sibmated	7	K159-19 X K159-21	1.5 c
S_2 sibmated	8	K159-21 X K159-19	1.5 c
S_1 X P (BC_1)	5	UH44-50 X Y166-1	1.9 c
P X S_2 (BC_2)	2	Y166-1 X K159-21	1.4 c
S_2 X P (BC_2)	9	K159-21 X Y166-1	1.9 c
Noninbred cross	10	2097-4N X K159-21	1.7 c

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least significant difference for multiple comparison testing.

[y]UH44 is the progeny of Y166-1 selfed.

[x]K159 is the progeny of UH44-50 selfed.

exhibited the highest percentage of bud drop per raceme, followed by the offspring of UH44-50 sibmated to UH44-5 (progeny 4).

The floral characters of scape length, raceme length, total initiated flowers, percent bud drop and vase life were not considered in the selection of the parental material. These characters in the progeny, in addition to showing no direction of selection, display no inbreeding effects. Use of a small number of individuals in creating an inbred line results in genetic drift (Svab, 1976); it appeared that the genetic make-up of the parental material seemed to determine the nature of these characters in each progeny. Should these characters also be of importance to the breeder, selection could be effective in increasing or decreasing these character values.

Yield

Progeny 10 produced the highest number of racemes every year from 1976 on (Table 10). Progenies 6, 7 and 8 yielded the fewest racemes every year. The other progenies did some switching in position order but generally remained intermediate.

The earliness to flower character, significantly later in the S_2 (progeny 3), S_3 (progeny 6) and S_2 sibbed (progenies 7 and 8) progenies than in the noninbred (progeny 10) and S_1 (progeny 1) progenies (Bobisud, 1976), is incorporated into the yield data. Later-flowering plants had the disadvantage of being compared with earlier-flowering progenies in total raceme production during a set period of time. However, it is believed that this late flowering

Table 10. Mean yield (number of harvested racemes) values of inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Yield 1975	Yield 1976	Yield 1977	Yield 1978	Total Yield
P selfed (S_1)	1	Y166-1 selfed	1.7 a[z]	5.9 bc	10.4 b	12.5 b	30.3 b
S_1 selfed (S_2)	3	UH44-5[y] selfed	0.6 cd	5.1 cde	10.7 b	12.0 bc	28.4 b
S_2 selfed (S_3)	6	K159-19[x] selfed	0.8 bcd	3.8 f	7.0 c	11.0 bc	22.5 c
S_1 sibmated	4	UH44-50 X UH44-5	1.1 b	6.2 ab	10.8 b	11.6 bc	29.7 b
S_2 sibmated	7	K159-19 X K159-21	0.6 cd	4.5 def	7.5 c	10.2 c	22.7 c
S_2 sibmated	8	K159-21 X K159-19	0.5 d	4.3 ef	7.8 c	11.2 bc	23.7 c
S_1 X P (BC_1)	5	UH44-50 X Y166-1	1.0 b	4.1 f	10.9 b	12.6 b	28.4 b
P X S_2 (BC_2)	2	Y166-1 X K159-21	0.9 bc	5.3 bcd	9.8 b	12.6 b	28.5 b
S_2 X P (BC_2)	9	K159-21 X Y166-1	1.1 b	5.6 bc	10.1 b	12.6 b	29.3 b
Noninbred cross	10	2097-4N X K159-21	1.0 b	7.0 a	14.7 a	14.8 a	37.5 a

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least significant difference for multiple comparison testing.

[y]UH44 is the progeny of Y166-1 selfed.

[x]K159 is the progeny of UH44-50 selfed.

during the years of low production was offset by the greatly increased yield of all plants in the later years.

Yield, a quantitative character, is an important agricultural consideration. The noninbred progeny yielded significantly more racemes than all other progenies while S_3 (progeny 6) and S_2 sibbed (progenies 7 and 8) progenies produced the fewest racemes. Thus, inbreeding depression was evident in yield. Interestingly, the S_1 (progeny 1) and S_2 (progeny 3) progenies did not statistically differ in yield. Selection for the vegetatively more vigorous plants at three growth stages represented selection pressure for vigor and hence, these offspring evaluated cannot be thought of as being entire progeny populations. Sampling error in the selection of the twenty plants of each progeny may have contributed, in part, to the yield data obtained. The decline in yield from the S_1 (progeny 1) to the S_3 (progeny 3), may reflect: (1) epistatic effects, whereby the accumulation of homozygous loci at the S_3 level displays a negative synergistic effect much greater in degree than at the S_2 level, (2) the different gene pools of UH44-5 and K159-19 (derived from UH44-50), (3) linkage of genes contributing to low yield with the genes for larger flower size and/or lower pink tinge, or (4) some combination of these effects. Greater reduction in yield, due to inbreeding, may have been alleviated by allopolyploidy having conferred a permanent-heterozygote condition due to interactions between homoeoalleles (Brown, 1972), since corresponding loci on homoeologous chromosomes may be of different alleles or possibly different genes (Sybenga, 1972).

Distribution of raceme production

Generally, most racemes are harvested from about May-June through September-October with a drop in production about July-August (Figures 5-14). Depending on the year, an earlier or later major harvest period was observed.

Of interest was a deviation from this pattern in progenies 3, 6 and 8 where only one major peak was observed in 1978. However, other progenies show less pronounced bimodality in 1978 in comparison to that of 1977. In 1977, there was a period of low production between the two peaks when it was observed that relatively few racemes were blooming in the saran house. In 1978, such an interim of low production was not observed. These two patterns of production peaks may be attributable to environmental differences in the two years or to different states of maturity of the plants.

Shoot height

Two different criteria were used in measuring plant height to see if different definitions would result in differences in significance. Height of the tallest shoot measures absolute height of the plant. The measurement of the most recently matured shoot involves a factor of time--newer shoots of approximately the same age are compared.

Using either criterion for shoot height measurement, the most inbred progenies (progenies 6, 7 and 8) were shortest (Table 11). The noninbred progeny (progeny 10) were amongst the taller progenies

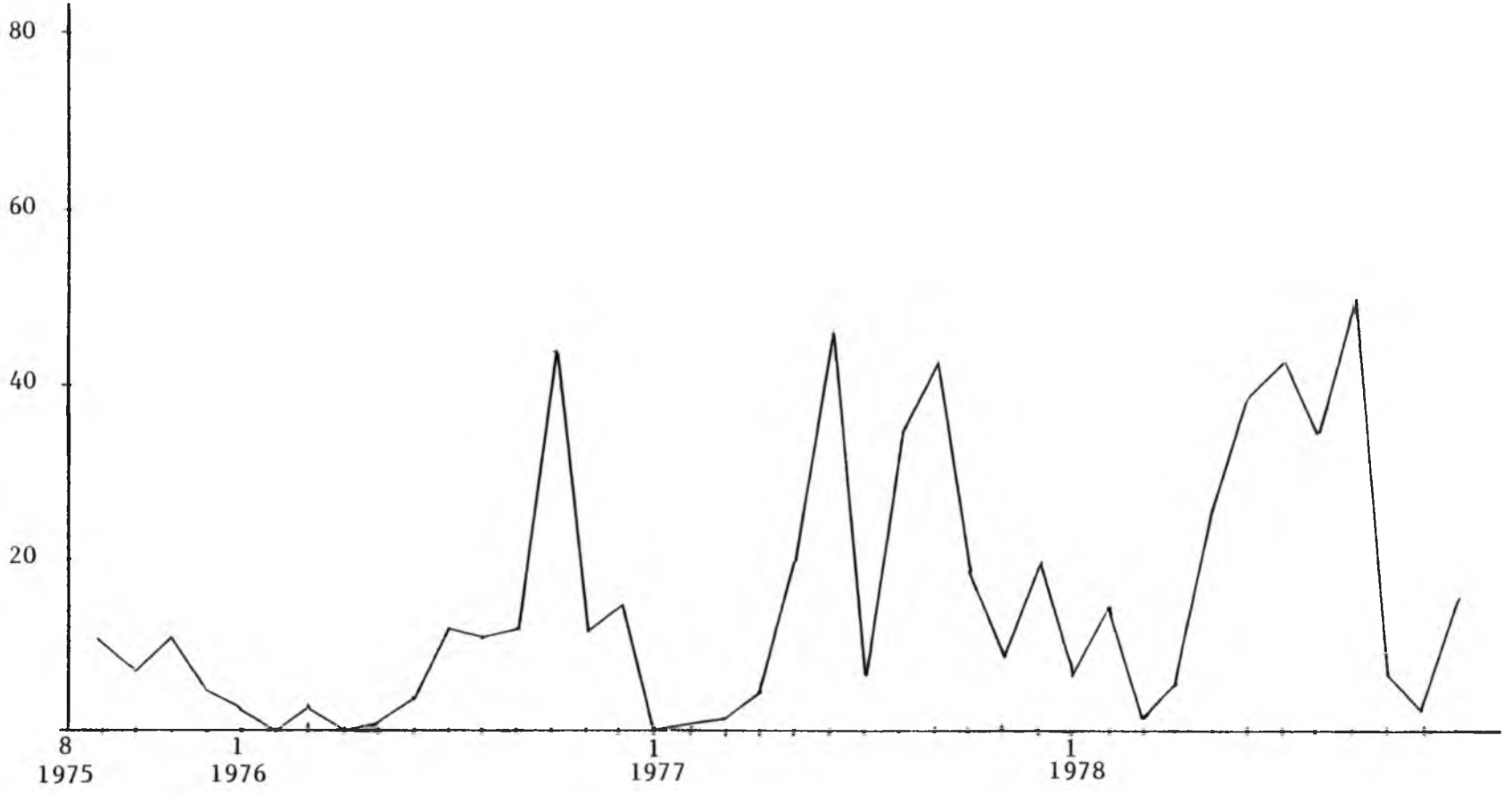

Figure 5. Distribution of racemes produced by progeny 1 (Y166-1 selfed) from August, 1975 to December, 1978.

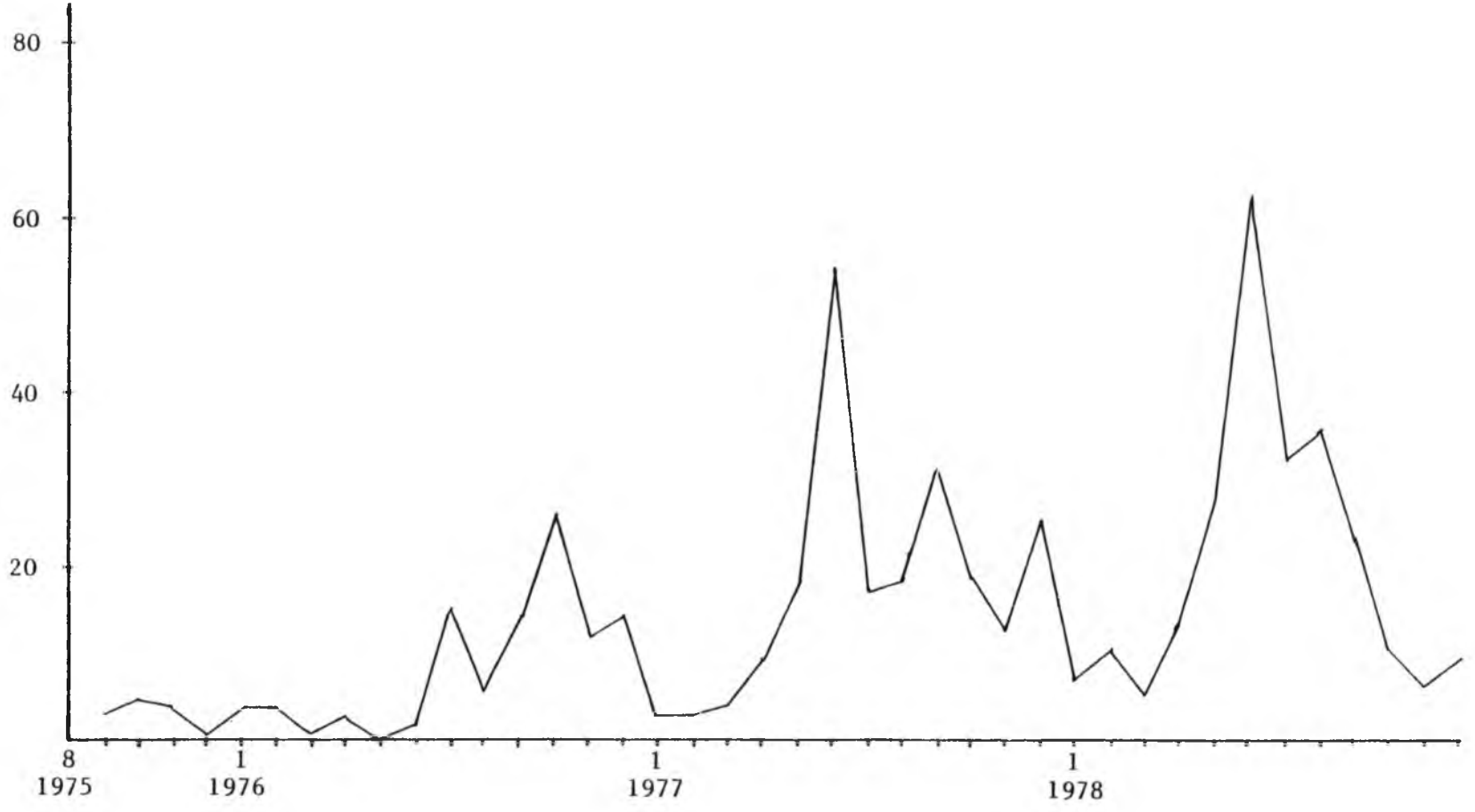

Figure 6. Distribution of racemes produced by progeny 3 (UH44-5 selfed) from August, 1975 to December, 1978.

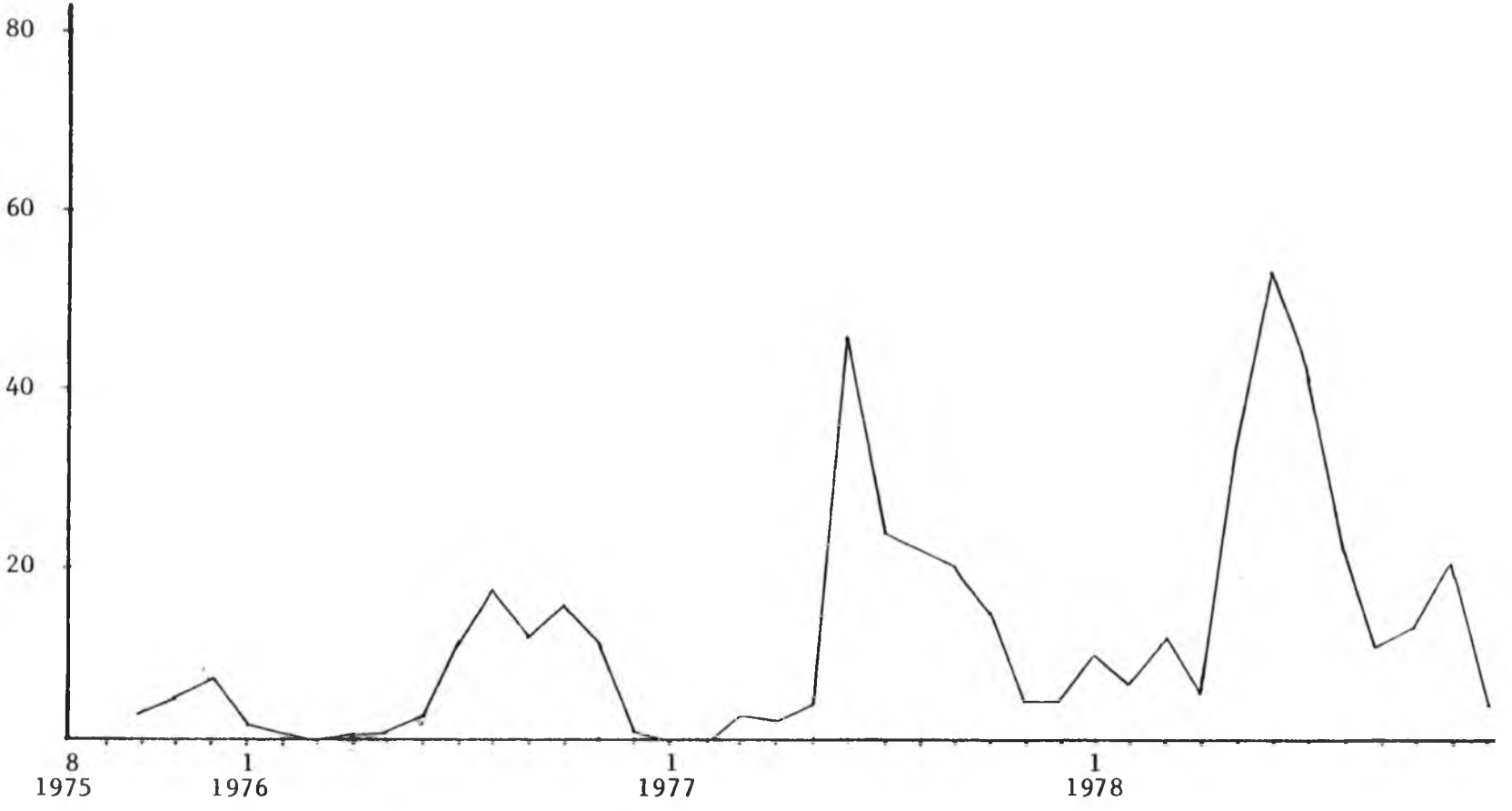

Figure 7. Distribution of racemes produced by progeny 6 (K159-19 selfed) from August, 1975 to December, 1978.

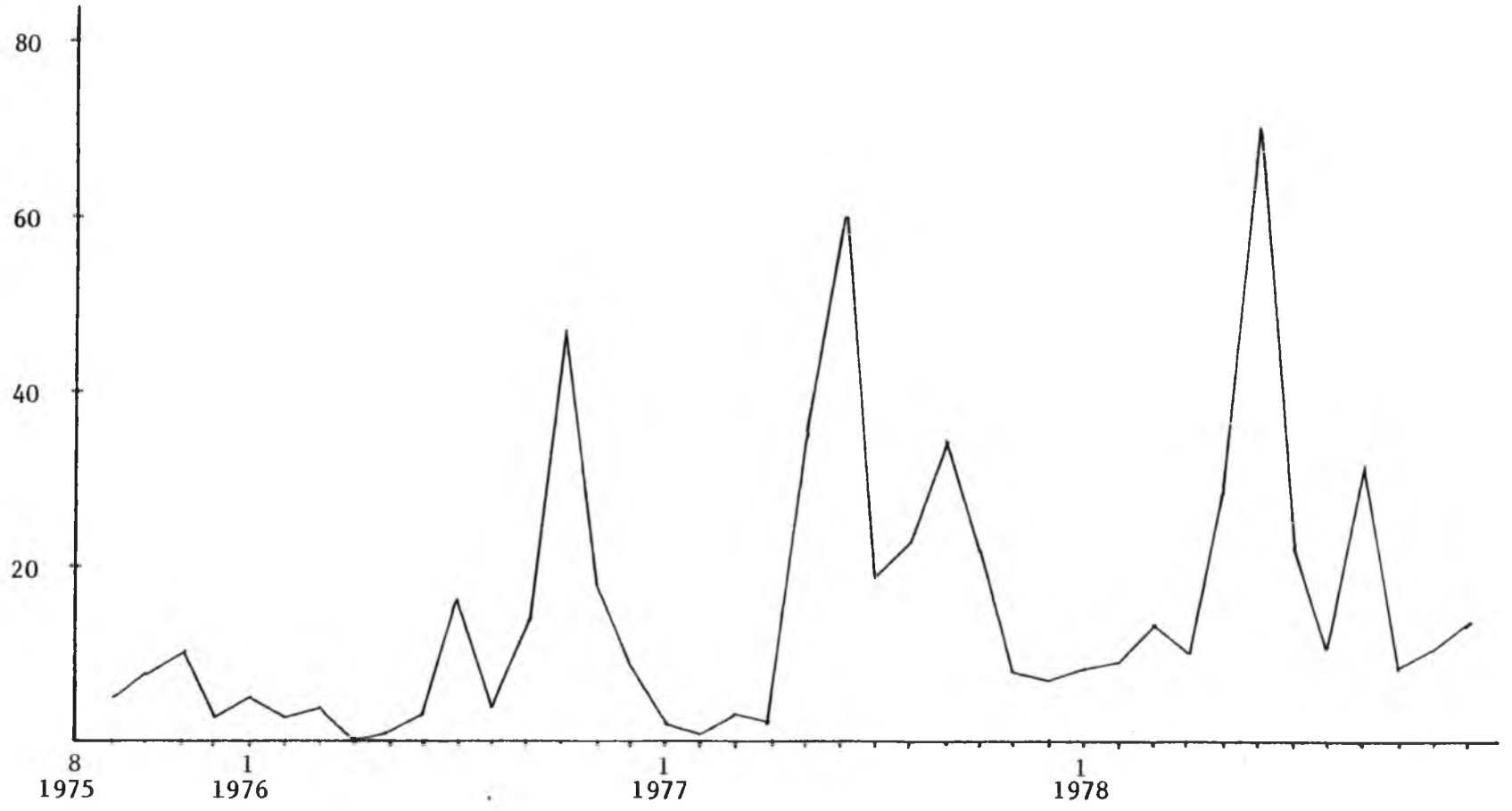

Figure 8. Distribution of racemes produced by progeny 4 (UH44-50 X UH44-5) from August, 1975 to December, 1978.

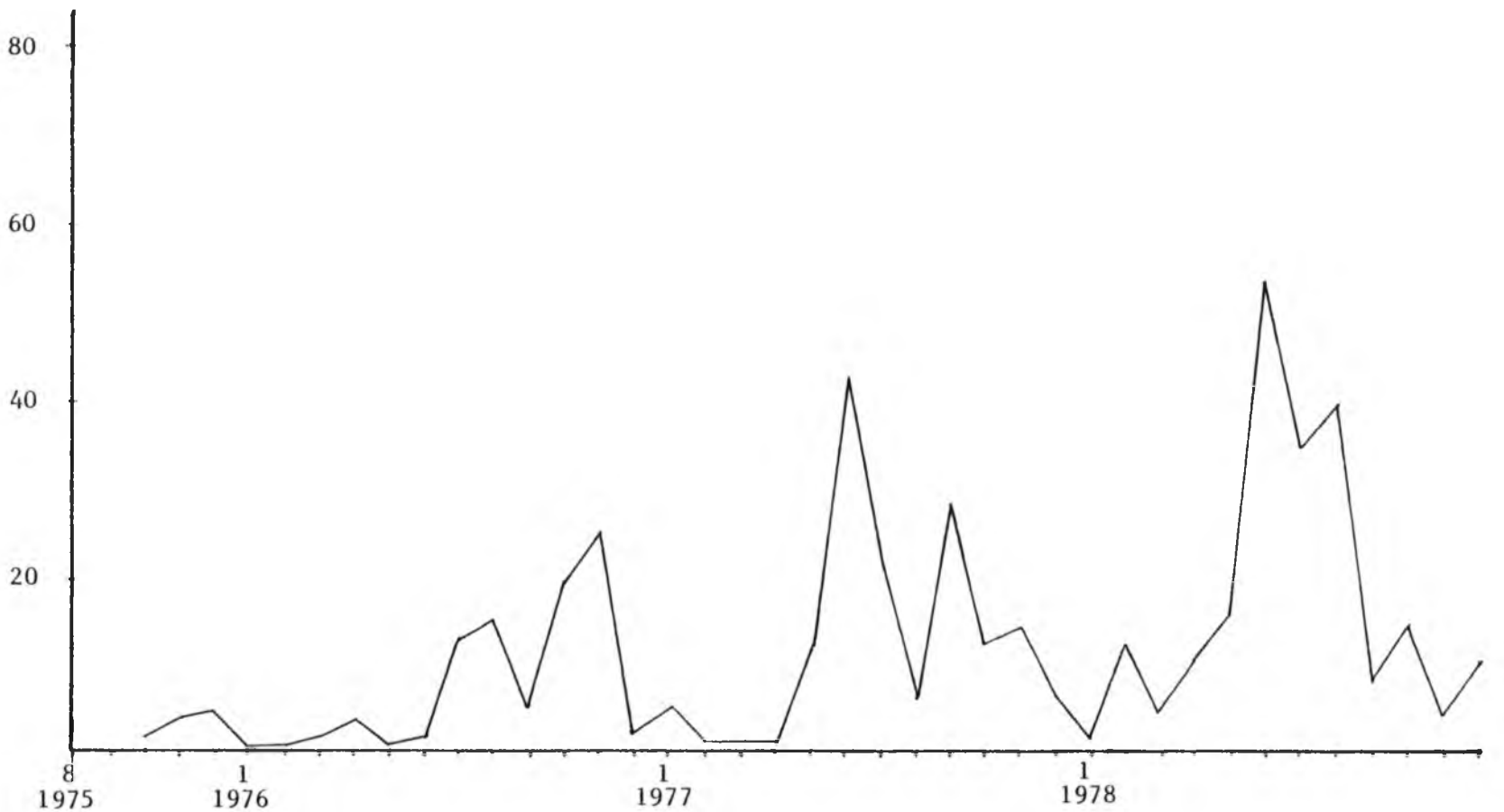

Figure 9. Distribution of racemes produced by progeny 7 (K159-19 X K159-21) from August, 1975 to December, 1978.

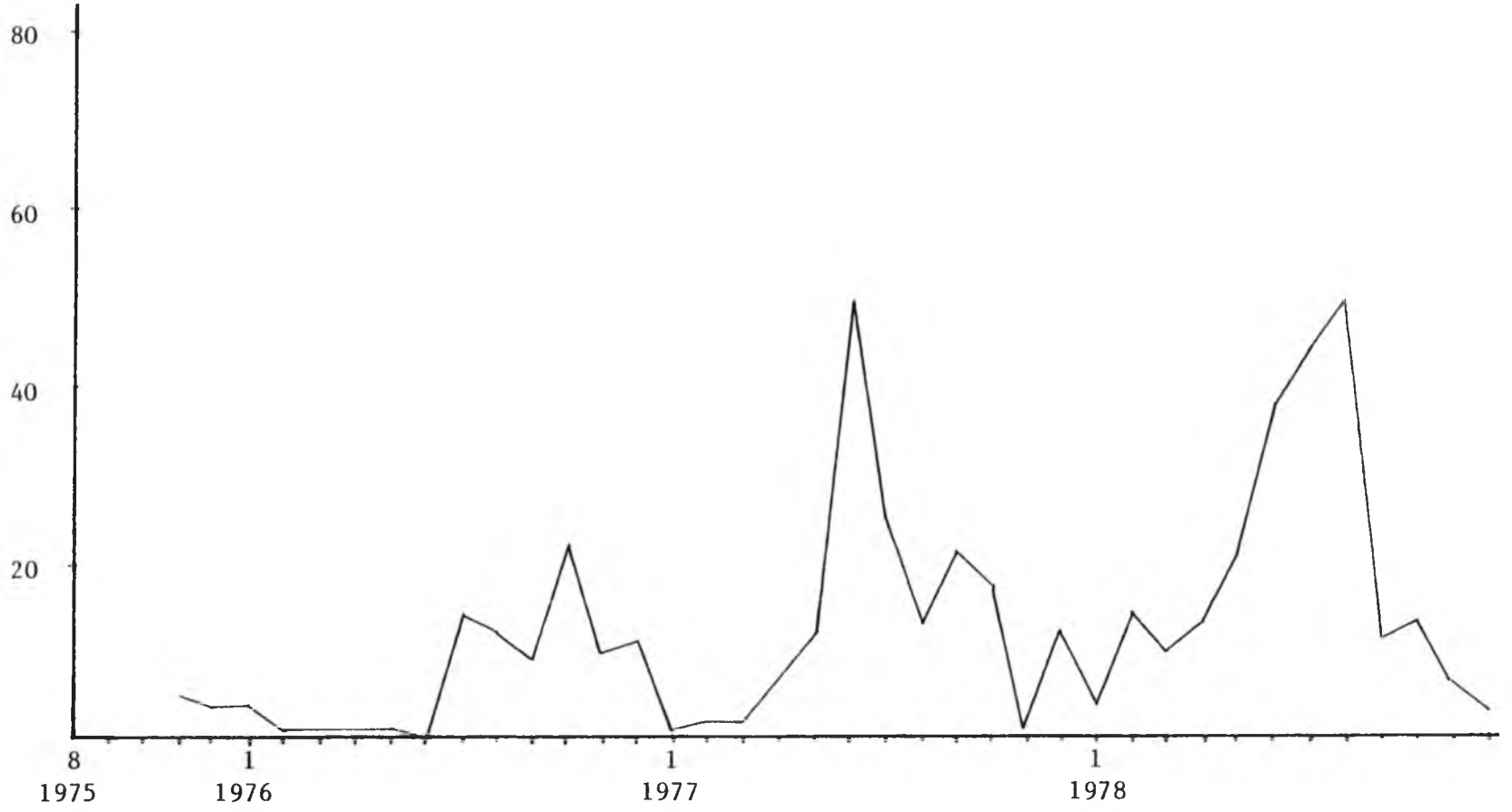

Figure 10. Distribution of racemes produced by progeny 8 (K159-21 X K159-19) from August, 1975 to December, 1978.

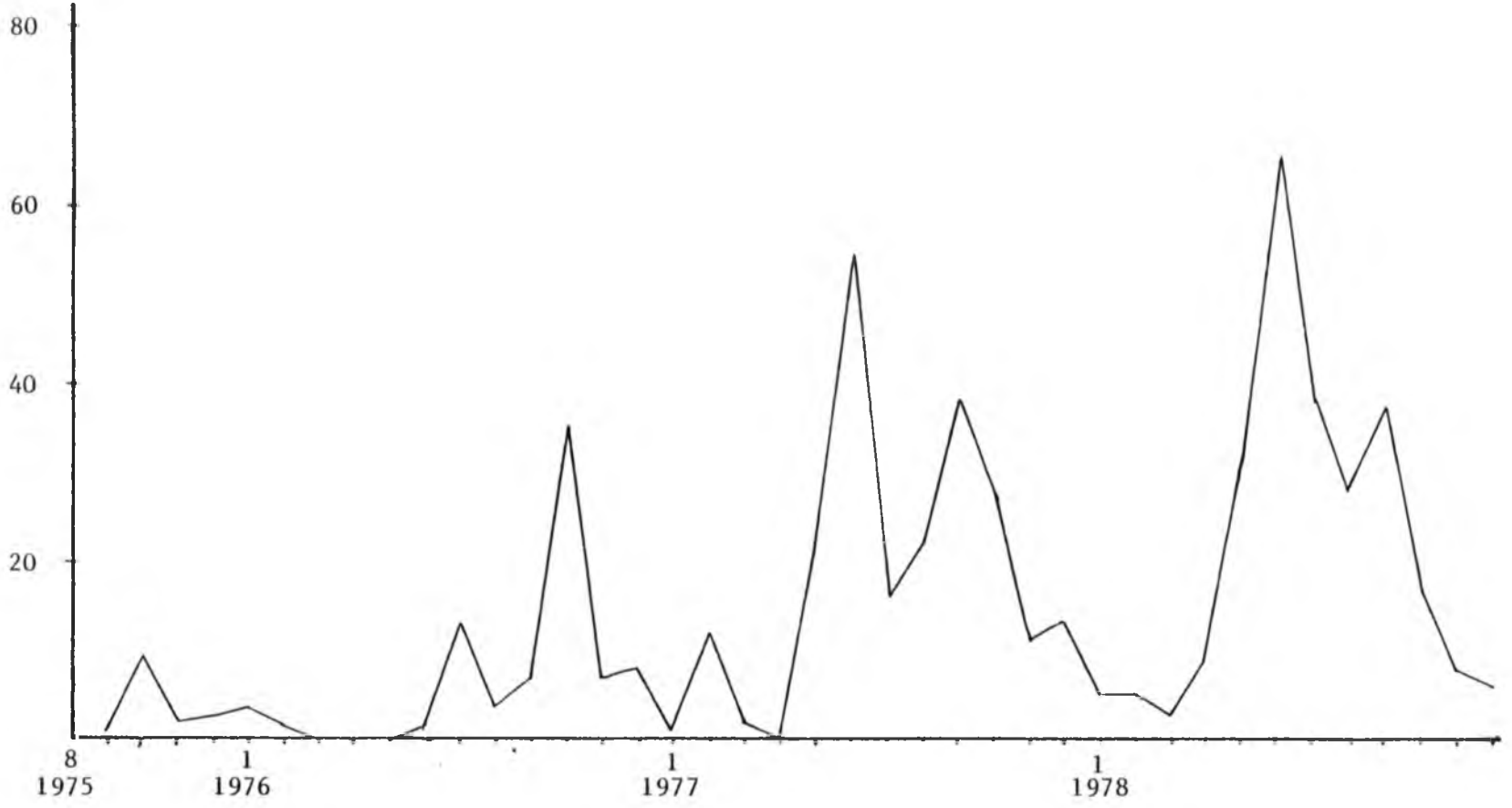

Figure 11. Distribution of racemes produced by progeny 5 (UH44-50 X Y166-1) from August, 1975 to December, 1978.

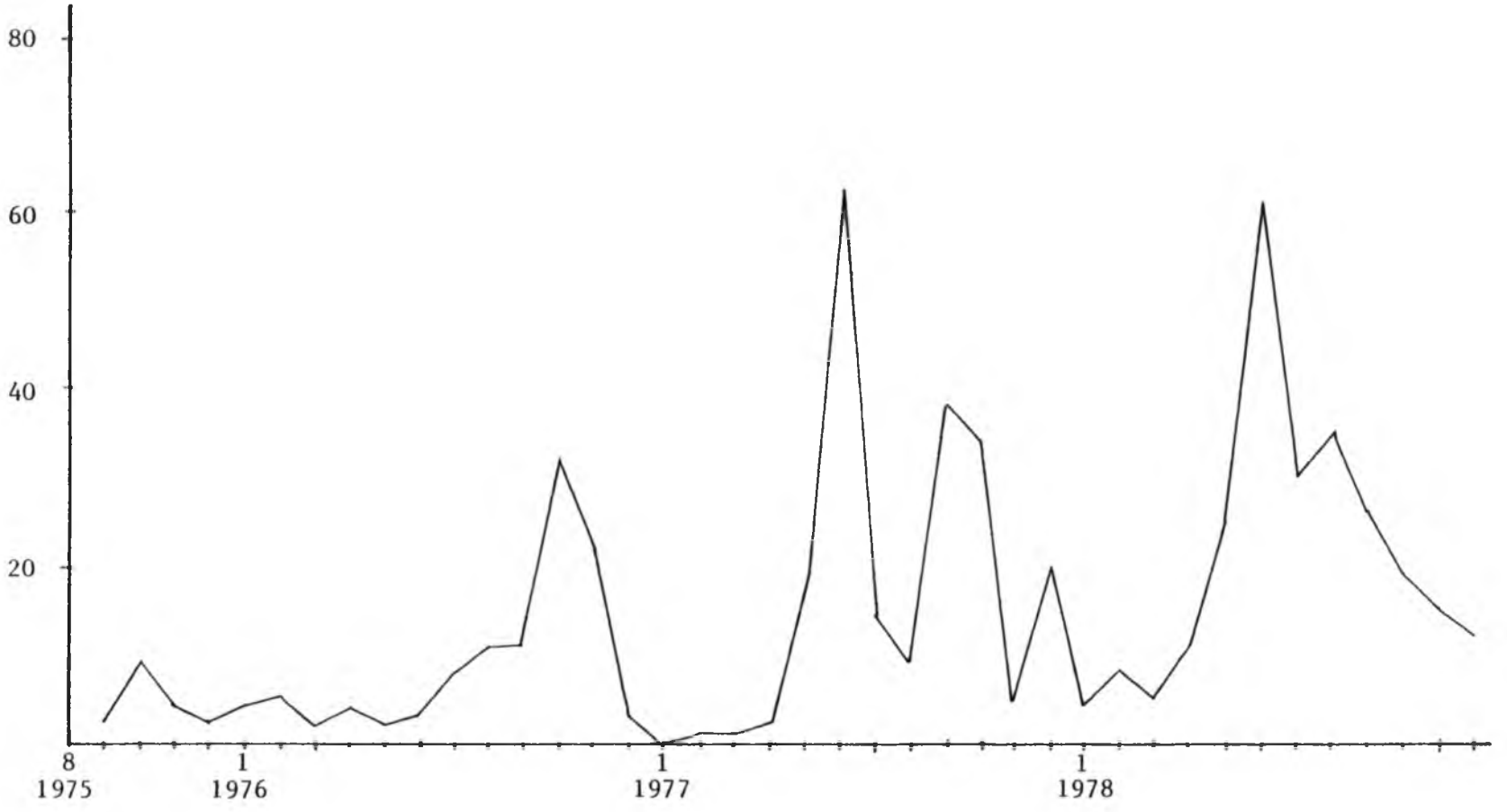

Figure 12. Distribution of racemes produced by progeny 2 (Y166-1 X K159-21) from August, 1975 to December, 1978.

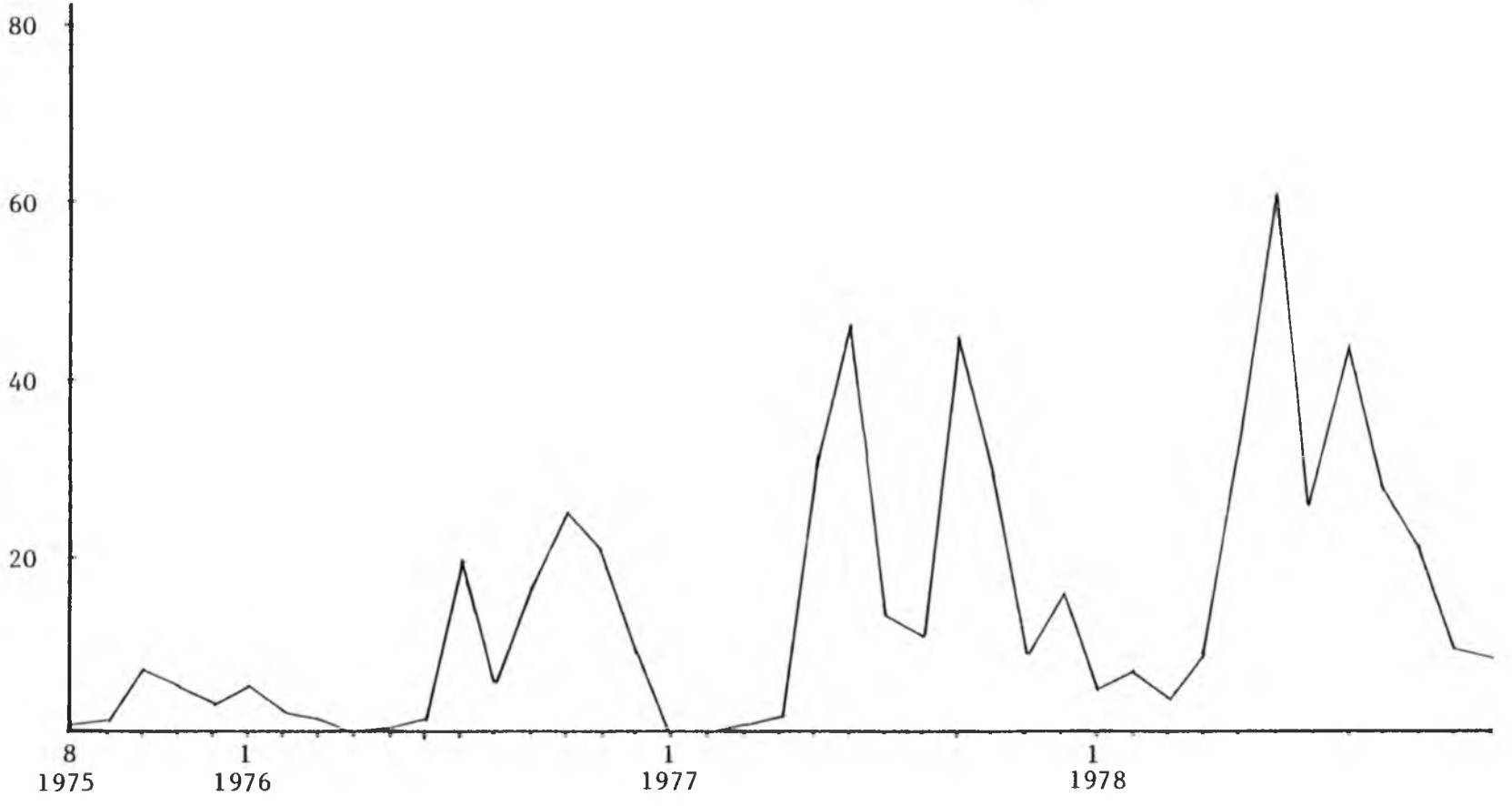

Figure 13. Distribution of racemes produced by progeny 9 (K159-21 X Y166-1) from August, 1975 to December, 1978.

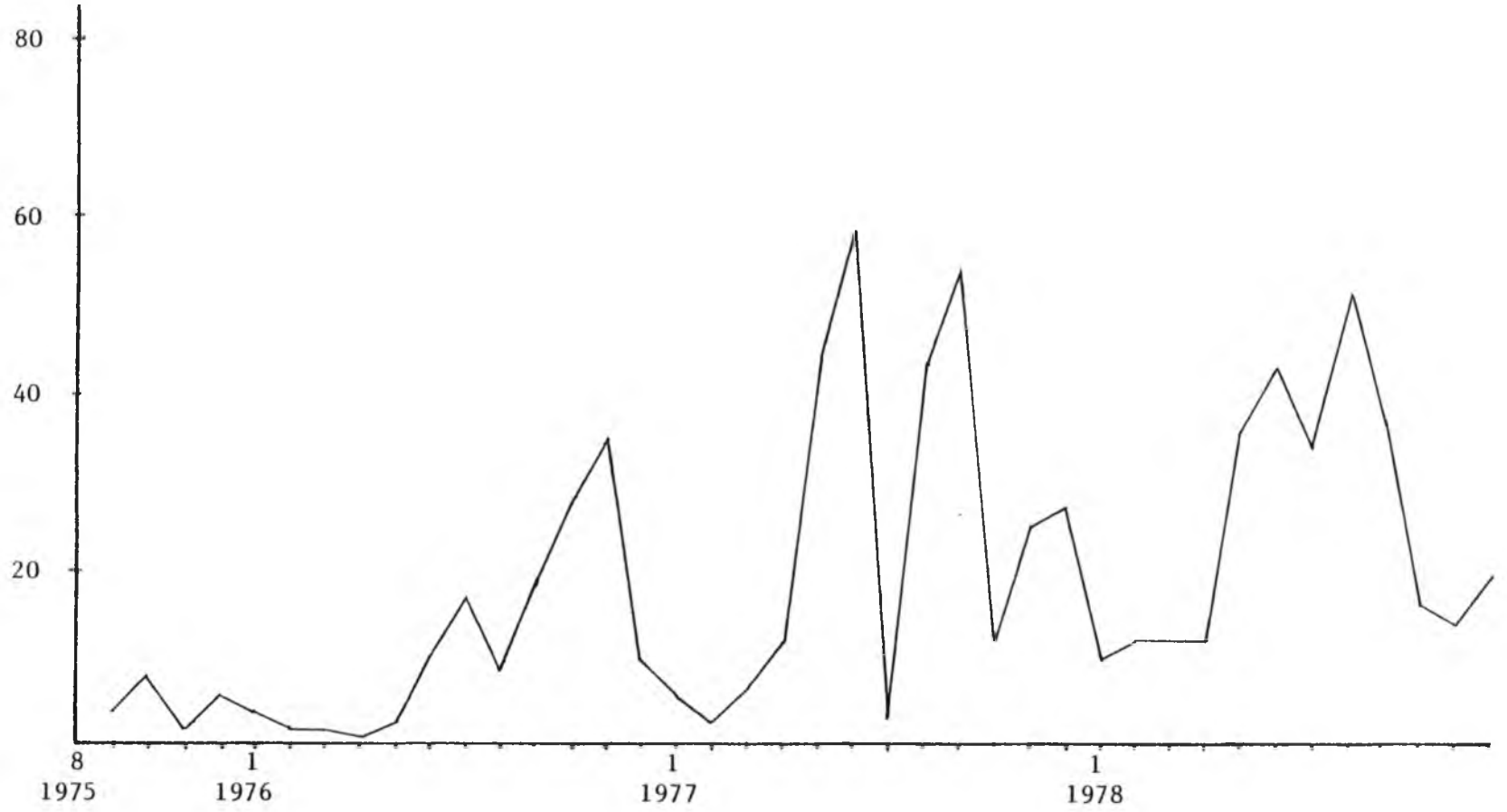

Figure 14. Distribution of racemes produced by progeny 10 (2097-4N X K159-21) from August, 1975 to December, 1978.

Table 11. Mean height values of progenies of inbred and noninbred matings of amphidiploid D. Jaquelyn Thomas and amphidiploid D. Neo Hawaii.

Type of Mating	Progeny Number	Individuals Mated	Height of Tallest Shoot (cm)	Height of the Most Recently Matured Shoot (cm)
P selfed (S_1)	1	Y166-1 selfed	136.3 a[z]	124.9 a
S_1 selfed (S_2)	3	UH44-5[y] selfed	139.3 a	128.8 a
S_2 selfed (S_3)	6	K159-19[x]	108.8 b	92.5 c
S_1 sibmated	4	UH44-50 X UH44-5	134.0 a	118.5 ab
S_2 sibmated	7	K159-19 X K159-21	111.9 b	100.0 c
S_2 sibmated	8	K159-21 X K159-19	106.9 b	96.1 c
S_1 X P (BC_1)	5	UH44-50 X Y166-1	135.8 a	125.1 a
P X S_2 (BC_2)	2	Y166-1 X K159-21	130.6 a	118.2 ab
S_2 X P (BC_2)	9	K159-21 X Y166-1	128.6 a	117.8 ab
Noninbred cross	10	2097-4N X K159-21	132.4 a	105.8 bc

[z]Means followed by the same letter in each column are not significantly different at P=0.05 by the Bayes least significant difference for multiple-comparison testing.

[y]UH44 is the progeny of Y166-1 selfed.

[x]K159 is the progeny of UH44-50 selfed.

in height of the tallest shoot, but were not significantly different from the shortest progenies in height of the most recently matured shoot.

The other progenies (progenies 1, 2, 3, 4, 5 and 9) did not differ from each other in height of the most recently matured shoot. They also did not differ significantly in height of the tallest shoot or from the tallest shoot of the noninbred progeny (progeny 10).

The shorter height measurement of the most recently matured shoot of the noninbred progeny (progeny 10) may be due to heavy raceme production at the expense of vegetative growth.

Using either definition of shoot height, the more inbred progenies, of S_3 (progeny 6) and S_2 sibbed (progenies 7 and 8), were the shortest. However, the noninbred cross was not significantly taller than the taller inbred progenies in one instance and actually among the shortest in the other. It is difficult to say whether the shortest progenies reflected inbreeding effects or the particular genotypic constitution of the particular plants selected for larger, whiter flowers. Since the noninbred progeny did not exceed all other progenies in height, heterosis is not obvious; thus, the character of shoot height possibly was influenced more by the genetic constitution of the parental plants than by the inbreeding process. However, selection of the vigorous individuals of each progeny for inclusion in this experiment may have negated inbreeding effects, and therefore, genotypic effects appeared more influential. While sympodial growth of the dendrobium plant generally results in successively taller shoots until a limit is attained, younger shoots

can be shorter than an older shoot. Such seems to be the case in the noninbred progeny where the most recently matured shoot had a mean height measurement lower than that of the tallest shoot. Possibly, the physiological "energy" of the plants may have been directed in other ways, such as raceme production in this high-yielding progeny, and thus, height of these later shoots were deprived of sufficient resources for growth.

Bench effects

Since the replicates were distributed on four benches within the saran house, it was of interest whether the differences in position in the saran house influenced the results. The characters of yield, vase life, percent bud drop per raceme, height of the tallest shoot, scape length, raceme length, flower size and the total number of initiated flowers were analyzed. Significant bench effects were found for vase life (Table 12).

Subsequent testing of the means by the Bayes least significant difference test showed that Bench 1 plants did give racemes of a longer mean vase life than did the plants on the other benches (Table 13). All this may indicate a tendency of the racemes on Bench 1 to be longer lasting due to the position of Bench 1, being directly next to one end of the saran house, or possibly to the sampling of replicates placed on Bench 1 since significant differences among replicates were found (Table 42).

Table 12. Significance of analysis of variance F values for bench effects on the characters of yield, vase life, percent bud drop per raceme, height of the tallest shoot, scape length, raceme length, flower size and total number of initiated flowers.[z]

Character	Significance of Bench Differences
Yield (number of harvested racemes)	n.s.
Vase life	*
Percent bud drop per raceme	n.s.
Height of tallest shoot	n.s.
Scape length	n.s.
Raceme length	n.s.
Flower size	n.s.
Total number of initiated flowers	n.s.

[z]Analyses of variance for these characters are found in Table 43.

n.s. means differences are nonsignificant at the 5% level.

*differences are significant at the 5% level.

Table 13. Mean values for yield, vase life, percent bud drop per raceme, height of the tallest shoot, scape length, raceme length, flower size and total number of initiated flowers of plants on each of four benches in the saran house.[z]

Bench	Yield (Number of Harvested Racemes)	Vase Life (Days)	Percent Bud Drop Per Raceme	Height of Tallest Shoot (cm)	Scape Length (cm)	Raceme Length (cm)	Flower Size (cm)	Total Number of Initiated Flowers
1	27.1	12.0 a[z]	2.7	125.1	19.26	64.89	6.07	20.8
2	28.7	11.3 b	2.0	130.1	18.51	63.21	6.08	20.6
3	27.4	11.3 b	2.2	121.9	18.56	63.16	6.03	20.7
4	29.1	11.4 b	2.5	128.6	18.78	64.29	6.09	20.7

[z]Each mean is the mean of 5 replicates situated on the respective benches.

[y]Means followed by the same letter in each column are not significantly different at P=0.05 by the Bayes least-significant difference for multiple-comparison testing.

Reciprocal crosses

Since reciprocal crosses do not always behave similarly in orchids, they were analyzed separately. However, no significant differences between reciprocal crosses were found for any of the characters analyzed.

1.3 Conclusion

Genetic variation exists among the S_1 progeny of Y166-1; this variation can be attributed to heterozygosity within the genomes of Y166-1 or to the occasional occurrence of allosyndesis in meiosis of Y166-1. Selection and inbreeding in D. Jaquelyn Thomas 'Y166-1' did direct a change toward a more desired extreme of the existing variation; selection for large flower size and lighter pink tinge in progenies from selfing Y166-1 and its descendants was successful in increasing flower size and flower color purity. Inbreeding decline was not observed in the characters of scape length, raceme length, number of initiated flowers, percent bud drop and vase life. Although sampling of vigorous individuals from each progeny possibly concealed some inbreeding effects evident in each entire population it was found that yield was reduced from the S_1 to the S_3. Inbred progenies descended from UH44-50, the S_1 individual selected for larger, whiter flowers, led to shorter plants.

CHAPTER II

INBREEDING EFFECTS ON THREE DIPLOID *DENDROBIUM* SPECIES AND AMPHIDIPLOID *DENDROBIUM* JAQUELYN THOMAS AT SEEDLING STAGE IN ASEPTIC CULTURE

2.1 Materials and Methods

Three different diploid *Dendrobium* species and two amphidiploid *D.* Jaquelyn Thomas hybrids were studied. *Dendrobium d'albertsii* plants from the S_1 (first generation of selfing) through the S_4 (fourth generation of selfing) were available, as were parental and S_1 plants of *D. schulleri* and *D. phalaenopsis*. *D.* Jaquelyn Thomas 'Y166-1' (from P to S_3) and '2085-4N' (P and S_1) were also available. These plants were selfed. Tables 14 and 15 detail the plants involved in the selfings.

Plants were selfed according to availability of flowers. Complete synchronization of pollinations within a species or a hybrid strain was not always possible.

Pods were harvested when they appeared to be sufficiently matured so that seeds would have separated from the placental tissue. Seeds from a pod were gently shaken into a 125 ml flask with the modified Vacin and Went germination medium (Table 23) in one layer in an attempt to minimize competition as the seeds germinated. Seeds from the same pod were sown into 6 flasks to insure against contamination or only fair germination. The seeds germinated and were transflasked when they were at the protocorm stage or the stage just beyond when they are just slightly differentiated. The

Table 14. Plants of Dendrobium species selfed to generate the progenies studied.

Species	Plant Number	Generation	Progeny Resulting from Selfing
D. d'albertsii	S1-10	S_1	S_2
	K73-1	S_2	S_3
	K176-8[z]	S_3	S_4
	K176-12	S_3	S_4
	K324-6[y]	S_4	S_5
	K324-20	S_4	S_5
	K325-10[x]	S_4	S_5
D. schulleri	D159	P	S_1
	K321-27	S_1	S_2
	K321-28	S_1	S_2
D. phalaenopsis	D40	P	S_1
	K133-1	S_1	S_2
	TO1-4	S_1	S_2
	TO1-3	S_1	S_2

[z]K176 is the progeny of K73-1 selfed.

[y]K324 is the progeny of K176-6 selfed.

[x]K325 is the progeny of K176-8 selfed.

Table 15. Dendrobium Jaquelyn Thomas plants selfed to generate the progenies studied.

Hybrid	Plant Number	Generation	Progeny Resulting from Selfing
D. Jaquelyn Thomas (Y166-1 strain)	Y166-1	P	S_1
	UH44-50	S_1	S_2
	1-6	S_1	S_2
	3-1	S_2	S_3
	K159-25	S_2	S_3
	3-16	S_2	S_3
	K159-21	S_2	S_3
	K159-19	S_2	S_3
	6-14	S_3	S_4
	6-10	S_3	S_4
	6-12	S_3	S_4
D. Jaquelyn Thomas (2085-4N strain)	2085-4N	P	S_1
	K241-5	S_1	S_2

protocorms were removed from the flask and put into 125 ml flasks containing 5 ml of sterile deionized water. The protocorms were swirled in the water and a miniature scoop was used to obtain a random sample of the protocorms. The protocorms were counted and imbedded into a small amount of germination medium which served as a carrier. Sampling was done until 60 protocorms had been counted. Protocorms were sampled from one flask unless only fair germination necessitated sampling from all 6 flasks. The 60 protocorms were transferred to a 500 ml flask containing modified Vacin and Went transflasking medium (Table 24) and then were spread out evenly on the medium surface. Seven replicates were made for each progeny, some less due to insufficient protocorms; contamination reduced the number of replicates in some cases. Seed sowing and transflasking were done under aseptic conditions. Care was taken so that the medium in all flasks was as uniform as possible.

The flasks of progenies of each species or hybrid were arranged separately in a randomized complete block design on racks. Blocks were situated so that flasks within the same block were the same distance from the light source directly above them. Flasks of different species or hybrids cannot be directly compared with each other since they were placed on different racks which constituted a different environment due to differences in the light source. Plants were grown under these conditions until their removal for drying and weighing. Replicates of D. d'altertsii and D. schulleri were divided into 2 parts--those dried and weighed 5 months after transflasking and those after 10 months. Since plant size was very

small at 5 months for D. Jaquelyn Thomas and D. phalaenopsis, drying and weighing of all replicates were done at 8-10 months.

Care needed to be exercised in selecting the plants to be dried. An attempt was made to remove plants individually from the flask with a large tweezer. Single plants with roots were chosen. Proliferated protocorms and seedlings were discarded. Plants without roots, in order to prevent confusion with a detached proliferation, were also discarded. Subjective decisions about which plants to include and which to discard were at times made, with the aim of keeping more than one of the same genotype from being included. Hence, the plants that were chosen for measurement were the single, rooted plants without much of a tendency toward proliferating.

The plants of a replicate were counted and placed in a paper bag which was then stapled shut. The paper bags were placed in a forced-draft oven at a temperature of 60 degrees C. for 4 days. Upon removal from the oven, the dried plant material from each paper bag was weighed on a Mettler analytical balance to the nearest ten-thousandth of a gram (nearest 0.1 mg).

Analysis of variance was done on the average individual plant weight per replicate. The Bayes least significant difference test was done where significant differences among progenies were found in the analysis of variance. The time involved in the procedures used is summarized in Table 16.

Table 16. Procedures performed on *Dendrobium* species and hybrid plants and the time elapsed between these procedures.

Species of Hybrid	Selfing Date(s)	Age of Pod when Sown for Germination (Months)	Assessment of Germination	Seed Sowing to Transflasking (Months)	Transflasking to First Dry Weight (Months)	Transflasking to Second Dry Weight (Months)
D. d'albertsii	May 17, 29 June 11, July 30, 1978	3	good	1	5	10
D. schulleri	June 11, 1978	3	good	2	5	10
D. phalaenopsis (Kosaki strain)	Nov. 21, Dec. 17, 1978, Feb. 13, 1979	4-5	poor to fair	3	8-10	
D. Jaquelyn Thomas (Y166-1 strain)	Oct. 24, Nov. 21, Dec. 8, 1978	4½-5½	good	2½	8	
D. Jaquelyn Thomas	Nov. 21, 28, 1978	5	good	2	10	

D. d'albertsii

D. d'albertsii plants were selfed on May 17, May 29, June 11 or July 30 in 1978, depending on the availability of flowers for pollination. Approximately 3 months later, in each case, seeds were aseptically sown for germination. Germination was good. About a month after the seeds were sown for germination, they were transflasked. At about 5 months after transflasking, replicates 1 to 3 were pulled and the plants in each replicate assessed and put in the oven to dry; replicates 1A to 4A were done about 10 months after transflasking. Both sets of replicates were analyzed separately.

D. schulleri

All self-pollinations were done on June 11, 1978. Sowing onto sterile media was done approximately 3 months later. Germination was good. Transflasking followed about 2 months afterward. Dry weights of plants in each of replicates 1 to 3 were obtained about 5 months after transflasking; the same was done to replicates 2A to 4A ten months after transflasking (replicate 1A was eliminated due to a contaminated flask within the replicate). Again, both sets of replicates were analyzed separately.

D. phalaenopsis (Kosaki strain)

These plants were selfed on November 21, December 17, 1978, or February 13, 1979, due to the unsynchronized flowering. Seeds were sown about 4-5 months after pollination; two pods each were sown for the selfings of D40 and K133-1. Germination was poor to fair. Approximately 3 months after the seeds were sown, transflasking was

done. Due to poor germination, only 3 replicates could be made of the progeny of TO1-3 selfed. About 8-10 months later, plants in all replicates were dried for weight measurements. Analysis was done as a completely randomized design.

D. Jaquelyn Thomas (Y166-1 strain)

Most of the self-pollinations of these amphidiploids were done on October 24, 1978; those plants not in flower at the time were selfed on November 21 or December 8, 1978 (UH44-5 could not be included because of a lack of flowers at the time). Four and a half to five and a half months subsequent to each date, the seeds were sown for germination; germination was good. About two and a half months after seed sowing, transflasking was done. About 8 months after transflasking, replicates 1-6 were prepared and dry weight measurements were taken. Analysis was performed on all 6 replicates.

D. Jaquelyn Thomas (2085-4N strain)

2085-4N is another amphidiploid plant which appeared from tissue culture of a diploid plant. Self-pollinations of these amphidiploid plants were done on November 21 or 28, 1978. The seeds were sown about 5 months later; germination was good. Transflasking was done two months following seed sowing. Ten and one half months later, the plants from the six replicates were removed from the flask, dried and weighed. All six replicates were analyzed together.

2.2 Results and Discussion

The limitations of the mean plant dry weight measurement of the seedlings at the flask stage are recognized--the range and distribution of the variation are not apparent. It was hoped that this mean plant dry weight measurement would approximate a population mean and would enable comparisons to be made among inbred progeny populations. However, sampling error may have played an important role in the results obtained, for proportionally only a small number of seedlings were grown relative to the thousands of seeds within each pod. Discarding proliferated plants, in an attempt to minimize confusion and to standardize the procedure, further reduced the number of plants; therefore, a few large plants or several really small plants could easily disturb the mean. Additionally, the early stage of growth of these seedlings may be a factor that prevents differences from being discerned. Hence, the data must be viewed cautiously.

Table 17 shows the significance of the differences in plant dry weight among the progenies within each species or hybrid strain. Tables 44 to 50 show the number of plants and dry weight of the plants from each flask. Tables 51 to 55 show the analysis of variance of the dry weight measurements.

D. d'albertsii

Table 18 contains the mean plant dry weight at 5 and 10 months after transflasking. Although the S_3 progeny of K73-1 had a low mean dry weight, analysis of variance showed no significant

Table 17. Significance of analysis of variance F values for mean plant dry weight of inbred progenies of different Dendrobium species and hybrids.

Species or Hybrid	Ploidy Level	Age (No. of Months after Transflasking)	Significance Among Progenies from Selfing	No. of Replicates
D. d'albertsii	2N	5	n.s.	3
		10	*	4
D. schulleri	2N	5	n.s.	3
		10	n.s.	3
D. phalaenopsis	2N	8-10	**	-
D. Jaquelyn Thomas (Y166-1 strain)	4N	8	**	6
D. Jaquelyn Thomas (2085-4N strain)	4N	10	n.s.	6

n.s. means not significant at P=0.05.

* significance at P=0.05, ** significance at P=0.01.

Table 18. Mean plant dry weight (mg) of each replicate and of all replicates of inbred progenies of D. d'albertsii.

Selfing	Generation of Progeny	5 Months After Transflasking				10 Months After Transflasking				
		Replicate			Mean Dry Weight of All Replicates	Replicate				Mean Dry Weight of All Replicates
		1	2	3		1A	2A	3A	4A	
S1-10 selfed	S_2	8.58	6.56	6.52	7.23	15.31	14.04	14.19	15.17	14.68 b[z]
K73-1 selfed	S_3	3.91	4.78	6.12	4.93	12.88	12.65	14.95	17.01	14.40 b
K176-12 selfed	S_4	8.17	8.00	6.04	7.40	13.63	21.28	22.18	20.77	19.48 ab
K176-8 selfed	S_4	5.55	8.36	7.30	7.10	12.88	22.40	23.12	36.40	23.70 a
K324-20 selfed	S_5	5.77	9.40	8.15	7.80	8.48	17.90	18.94	16.50	15.45 b
K325-10 selfed	S_5	6.87	7.22	8.13	7.40	14.93	15.61	15.97	14.93	15.35 b
K324-6 selfed	S_5	6.84	8.71	7.92	7.80	13.32	19.04	19.02	18.85	17.53 b

[z]Means followed by the same letter in each column are not significantly different at P=0.05 by the Bayes least-significant difference for multiple-comparison testing.

differences among the progenies at 5 months after transflasking (Table 51) while one of the S_4 progenies (K176-8 selfed) had a significantly (5% level) higher mean dry weight than did the other generations of progenies at 10 months after transflasking (Table 18). Visual inspection of the flasks and the removed plants showed a small variation in plant size. This was contrary to what was observed in flasks of the other species or hybrids where great variation in plant size was noted.

The S_2, S_3, S_4 and S_5 progenies of D. d'albertsii (except for one S_4 progeny) did not differ in mean plant dry weight. An interesting observation made was that there was relative uniformity in plant size within and among the flasks of D. d'albertsii. The range in plant size was small. It has been observed that full-grown inbred plants of D. d'albertsii do not display inbreeding degeneration with each successive generation of selfing; pods have also been observed to set naturally, perhaps sometimes resulting from self-pollination (H. Kamemoto, personal communication). Therefore, the original genetic constitution of this particular D. d'albertsii line may have been sufficiently homozygous for favorable growth genes for it to display little or no inbreeding decline as well as a tendency toward being self-pollinating. According to Stebbins (1957), a tendency toward self-pollination can arise from isolated conditions of cultivated plants and also in the absence of insect pollinators.

D. schulleri

A lot of proliferations were observed in flasks of D. schulleri. Visual inspection showed great variation among the replicates in terms of plant size and the amount of proliferations from protocorms. Many proliferated plants had to be discarded and therefore, small numbers of plants per flask were left for measurement. Table 19 shows the dry weight data. Analysis of variance (Table 52) showed no differences among the S_1 and S_2 progenies. Despite the small number of plants salvaged for drying and weighing, K321-27 selfed produced progeny with the lowest average plant weight at 5 months and 10 months after transflasking.

In the inbred progenies of D. schulleri, there was a tendency to proliferate in this medium. The small number of plants salvaged made it difficult to assess differences among the S_1 and S_2 progenies. Also, the great variation among plants within a flask and among replicates probably precluded any differences being detected.

D. phalaenopsis (Kosaki strain)

S_2 progeny of T01-3 selfed displayed low vigor when the number of germinated seedlings were insufficient for 6 replicates--only 3 replicates were made. Therefore, analysis was done as a completely randomized design (Table 53). Table 20 shows dry weight measurements for each flask. S_2 progenies of T01-3 selfed and of T01-4 selfed were significantly lower in dry weight than the S_1 progeny of D40 selfed (Table 20). The S_2 progeny of K133-1 selfed was not significantly different from the S_1 progeny of D40 selfed in dry weight.

Table 19. Mean plant dry weight (mg) of each replicate and of all replicates of inbred progenies of *D. schulleri*.

Selfing	Generation of Progeny	5 Months After Transflasking				10 Months After Transflasking			
		Replicate			Mean Dry Weight of All Replicates	Replicate			Mean Dry Weight of All Replicates
		1	2	3		1A	2A	3A	
D159 selfed	S_1	2.49	1.44	2.09	2.01	3.54	8.39	5.58	5.84
K321-27 selfed	S_2	1.64	1.63	1.71	1.66	2.99	6.51	6.71	5.40
K321-28 selfed	S_2	2.14	1.22	3.75	2.37	2.88	6.26	12.56	7.23

Table 20. Mean plant dry weight (mg) of each replicate (flask) and of all replicates if inbred progenies of Dendrobium phalaenopsis (Kosaki strain) at 8-10 months after transflasking.

Selfing	Generation of Progeny	Replicate						Mean Dry Weight of All Replicates
		1	2	3	4	5	6	
D40 selfed	S_1	21.39	21.76	20.26	24.12	21.31	24.05	22.15 a[z]
K133-1 selfed	S_2	23.52	26.76	24.79	20.18	25.95	21.09	23.72 a
TO1-4 selfed	S_2	12.70	17.97	12.22	14.02	20.54	16.75	15.70 b
TO1-3 selfed	S_2	14.90	15.08	17.86	-	-	-	15.95 b

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least-significant difference for multiple-comparison testing.

The D. phalaenopsis 'Kosaki' S_2 progenies from TO1-4 and TO1-3 with equal degree of inbreeding did not differ from each other and were significantly lower in measurements than the progenies of D40 selfed (S_1) and K133-1 selfed (S_2). The high dry weight measurement of the S_2 progeny of K133-1 may have been partly due to the genotypic constitution of K133-1. Unlike D. d'albertsii, which has been inbred for 5 generations without apparent loss in vigor, D. phalaenospis has shown inbreeding effects in mature plants. It has not been possible to go beyond the S_2 generation because the mature S_2 plants have been weak and have failed to produce viable offspring (H. Kamemoto, personal communication).

D. Jaquelyn Thomas (Y166-1 strain)

Table 21 shows the average plant dry weight per flask and the mean plant dry weight for all replicates. Analysis of variance showed significant differences among progenies (Table 54). The S_2 progeny from 1-6 had the highest mean dry weight while the S_4 progeny of 6-14 had the lowest. The S_1 progeny of the parent Y166-1 did not differ significantly from the S_4 progeny of 6-14 but was significantly less than the S_4 progeny of 6-10. Most of the progenies originating from UH44-50 (6-10 selfed, UH44-50 selfed, 6-12 selfed, K159-21 selfed and K159-19 selfed) did not differ very much from one another, with the progeny of 6-10 selfed being significantly higher in mean plant dry weight than the progeny of K159-19 selfed; progenies of K159-25 selfed (not differing from that of 159-19 selfed) and of 6-14 selfed had the least mean dry weight. The S_2 progeny of 1-6 selfed was

Table 21. Mean plant dry weight (mg) of each replicate (flask) and of all replicates of inbred progenies of D. Jaquelyn Thomas (Y166-1 strain) at 8 months past transflasking.

Selfing	Generation of Progeny	Progenitor of Plant Being Selfed	Replicate						Mean Dry Weight of All Replicates
			1	2	3	4	5	6	
Y166-1 selfed	S_1	-	5.32	4.08	5.38	4.42	3.65	2.61	4.23 efg[z]
UH44-50 selfed	S_2	Y166-1	4.50	6.02	6.69	6.88	6.42	3.96	5.75 bcd
1-6 selfed	S_2	Y166-1	7.47	10.41	8.97	6.53	5.67	5.70	7.47 a
3-1 selfed	S_3	UH44-5	5.53	6.52	6.03	3.96	4.91	4.08	5.17 cde
K159-25 selfed	S_3	UH44-50	4.35	4.68	2.95	2.68	3.39	2.57	3.45 fg
3-16 selfed	S_3	UH44-5	6.43	8.18	8.46	4.23	8.97	4.43	6.78 ab
K159-21 selfed	S_3	UH44-50	4.28	6.23	4.64	5.33	6.63	3.05	5.02 cde
K159-19 selfed	S_3	UH44-50	6.55	4.58	2.20	4.96	6.15	2.74	4.55 def
6-14 selfed	S_4	K159-19	2.82	3.43	3.35	3.33	4.22	1.72	3.12 g
6-10 selfed	S_4	K159-19	7.04	8.86	5.33	5.06	5.47	4.28	6.02 bc
6-12 selfed	S_4	K159-19	4.84	5.22	8.59	2.92	4.98	3.96	5.08 cde

[z]Means followed by the same letter are not significantly different at P=0.05 by the Bayes least-significant difference for multiple-comparison testing.

significantly different from the S_2 progeny of UH44-50 selfed. Among the S_3 progenies, that of 3-16 selfed (derived from the S_1 plant UH44-5) had a significantly higher mean dry weight while the progeny of 3-1 selfed (also derived from the S_1 plant (UH44-5) did not differ from two S_3 progenies derived from UH44-50 of the S_1. Of the S_4 progenies, all having been derived from K159-19 of the S_2, the progeny of 6-14 selfed had the lowest mean dry weight. Unsynchronized growth periods as well as the larger number of progenies prevented direct visual comparisons from being made at the time of drying.

Since inbreeding decline may not be as readily apparent in the inbred progenies of D. Jaquelyn Thomas 'Y166-1', the genetic constitutions of those individuals used to generate these progenies may have been responsible for the lack of any pattern of inbreeding decline at this stage of growth. It was thought that dry weight measurements in the flasks might be comparable to the vegetative character of height in the later stages of growth, but height data in experiment 1 seem to show some decline with increased inbreeding--this is not the case with the dry weight data.

D. Jaquelyn Thomas (2085-4N strain)

Table 22 shows the mean plant dry weights for each flask and for all replicates. No significant differences (Table 55) were found between S_1 and S_2 progenies.

The lack of detected difference between the S_1 and S_2 progenies of D. Jaquelyn Thomas '2085-4N' may possibly be due to the particular genetic constitution of the S_1 individual generating the S_2 progeny,

Table 22. Mean plant dry weight (mg) of each replicate (flask) and of all replicates of inbred progenies of D. Jaquelyn Thomas (2085-4N strain) at 10 months past transflasking.

Selfing	Generation of Progeny	Replicate						Mean Dry Weight of All Replicates
		1	2	3	4	5	6	
2085-4N selfed	S_1	22.07	22.57	20.62	20.28	23.05	19.99	21.45
K241-5 selfed	S_2	19.82	21.22	19.53	23.98	18.51	20.38	20.57

to amphidiploidy contributing some heterozygosity effect, as mentioned in the previous chapter, or to the early growth stage of the plants.

Mean plant dry weight, used as a measurement of growth to assess differences in vigor among the selfed progenies of selfing, was not as successful an indicator as hoped. Genotypes of this normally cross-pollinated material which were used as parents probably affected the character of the progeny populations. The limited number of individuals used as parents further affected the data. Plants in the flask stage may be too early in growth and development to be successfully evaluated for differences in growth. The relatively small number of plants grown (in comparison to the number of seeds within a pod) may have led to sampling error being an influential factor. Also, conditions within the flask--e.g., greenhouse or saran house conditions. Progenies which grow well in the sterile environment within the flask may not do as well in the greenhouse. Therefore, the effects of an overall increase in homozygosity due to inbreeding could not be easily evaluated in each species or hybrid.

When the degree of inbreeding of a naturally cross-pollinated plant is not too intense, some range in variation is existent in the progeny population from selfing. The breeder can select within this range for his own purposes, be it for breeding or for cultivation; the intensity of selection can be controlled. Horticulturally, inbred populations of dendrobiums need not be dealt with in entirety--merely the most vigorous portion of the population may be chosen for cultivation.

2.3 Conclusion

The original diploid D. d'albertsii plant produced 5 generations of progenies which showed no inbreeding depression in the flask stage of growth. Due to a tendency to proliferate, it was difficult to assess differences among inbred progenies of D. schulleri. D. phalaenopsis 'Kosaki' S_2 progenies from T01-4 and T01-3 gave significantly lower dry weight measurements than the S_1 progeny from D40. The S_2 progeny from K133-1 did not differ in dry weight measurements from the S_1 progeny from D40. No inbreeding depression was found among the inbred progenies of amphidiploid D. Jaquelyn Thomas 'Y166-1'. It may be that amphidiploidy prevented any decline from being detected and that sampling error was responsible for the results obtained. No dry weight difference was found in the flask stage of growth between the S_1 and S_2 progenies of amphidiploid D. Jaquelyn Thomas '2085-4N'.

APPENDIX

Table 23. Modified Vacin and Went culture medium for germination of orchid seeds.

Constituent	Chemical Formula	Quantity
Tricalcium phosphate	$Ca_3(PO_4)_2$	0.20 grams
Potassium nitrate	KNO_3	0.525 "
Monopotassium acid phosphate	KH_2PO_4	0.25 "
Magnesium sulfate	$MgSO_4 \cdot 7H_2O$	0.25 "
Ammonium sulfate	$(NH_4)_2SO_4$	0.50 "
Iron chelate (Sequestrene 330 Fe) stock solution*+		5 milliliters
Manganese sulfate	$MnSO_4 \cdot H_2O$	0.0057 grams
Sucrose		20.00 "
Agar*		9.00 "
Water*		850 milliliters
Coconut water*		150 milliliters

*Modified constituents

+Stock solution = 1.14 gm iron chelate per 100 ml

Table 24. Modified Vacin and Went culture medium for transflasking of orchid seedlings.

Constituent	Chemical Formula	Quantity
Tricalcium phosphate	$Ca_3(PO_4)_2$	0.20 grams
Potassium nitrate	KNO_3	0.525 "
Monopotassium acid phosphate	KH_2PO_4	0.25 "
Magnesium sulfate	$MgSO_4 \cdot 7H_2O$	0.25 "
Ammonium sulfate	$(NH_4)_2SO_4$	0.50 "
Iron chelate (Sequestrene 330 Fe) stock solution*+		5 milliliters
Manganese sulfate	$MnSO_4 \cdot H_2O$	0.0057 grams
Sucrose		10.00 "
Agar*		9.00 "
Water*		850 milliliters
Coconut water*		150 milliliters
Williams hybrid banana*		100 grams

*Modified constituents.

+Stock solution = 1.14 gm iron chelate per 100 ml.

Table 25. 1975 yield (number of harvested racemes) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	2	1	2	0	1	1	1	0	2	2
2	2	1	1	2	1	1	0	1	1	1
3	1	1	2	2	1	1	1	1	1	1
4	2	1	0	2	1	2	1	1	1	1
5	2	3	0	2	0	0	0	0	1	1
6	2	0	0	1	4	1	0	1	1	1
7	1	1	0	0	1	1	1	1	1	2
8	2	1	1	1	2	1	1	1	2	1
9	2	1	1	2	1	0	0	1	2	0
10	1	1	0	1	1	1	0	1	0	1
11	3	1	1	1	1	1	0	0	0	1
12	1	1	1	2	1	1	1	1	0	1
13	2	1	2	1	1	0	1	0	1	1
14	1	1	0	1	1	0	0	0	1	0
15	2	0	1	1	1	0	1	0	1	1
16	1	0	0	1	0	1	1	0	0	1
17	3	0	0	1	1	1	1	0	1	0
18	1	0	1	1	0	1	0	0	2	2
19	1	1	0	0	0	1	1	0	2	1
20	1	1	0	0	0	0	0	0	1	1

Table 26. 1976 yield (number of harvested racemes) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	5	5	8	7	7	8	7	5	6	8
2	8	7	6	9	5	3	8	8	6	8
3	9	7	5	8	3	4	7	4	7	8
4	4	4	7	7	2	3	7	4	5	6
5	5	6	3	9	6	6	3	4	5	9
6	4	7	5	7	2	4	5	4	6	7
7	7	7	3	4	4	4	6	5	5	4
8	7	7	2	5	2	4	3	5	5	7
9	3	6	7	7	4	3	3	5	6	5
10	4	5	0	6	3	3	2	5	2	7
11	6	6	4	8	5	4	8	3	6	9
12	8	5	7	4	7	4	6	7	7	9
13	4	7	6	4	5	4	5	4	7	9
14	5	6	6	4	5	3	0	0	4	3
15	6	4	5	5	4	3	3	5	8	9
16	6	5	8	5	5	4	4	1	5	8
17	5	2	5	5	2	3	1	2	2	5
18	7	3	5	4	3	3	2	4	8	4
19	5	4	7	9	3	2	3	6	6	6
20	9	3	2	7	5	3	7	5	6	9

Table 27. 1977 yield (number of harvested racemes) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	12	7	9	8	14	5	5	10	13	13
2	13	10	7	10	9	8	10	11	9	15
3	9	12	9	14	4	8	6	6	12	10
4	10	10	21	11	6	6	8	6	8	12
5	15	12	26	12	15	10	6	8	7	17
6	8	12	9	18	13	8	6	8	14	14
7	13	8	16	10	9	10	10	7	10	17
8	8	7	8	11	13	6	4	10	6	22
9	5	11	8	8	10	5	8	10	9	13
10	12	8	9	10	11	4	7	7	13	12
11	9	12	9	13	10	7	9	3	8	15
12	7	8	8	12	8	7	6	8	7	14
13	14	7	8	11	6	5	7	6	11	15
14	7	10	14	8	9	8	3	6	12	9
15	10	7	8	10	10	8	16	7	5	12
16	11	12	14	10	12	8	5	6	8	21
17	11	10	6	8	18	4	8	10	14	18
18	8	14	10	10	16	7	11	7	15	17
19	12	7	9	6	16	5	6	10	9	19
20	13	11	6	16	9	10	8	10	11	9

Table 28. 1978 yield (number of harvested racemes) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	12	12	14	16	15	11	4	14	10	17
2	12	16	11	10	13	13	11	14	12	17
3	10	15	8	12	8	13	6	14	10	17
4	19	13	16	9	11	9	13	11	19	20
5	12	12	18	10	14	12	12	9	11	20
6	10	11	15	11	12	10	14	11	11	15
7	13	8	10	9	11	16	14	11	10	11
8	16	15	11	17	14	12	7	14	13	15
9	8	7	12	14	9	9	13	8	13	14
10	12	11	11	16	11	12	8	10	14	14
11	15	14	9	10	12	16	11	8	8	15
12	13	10	9	12	15	9	9	8	14	14
13	12	14	11	6	13	10	12	10	14	18
14	10	12	10	12	18	10	6	12	13	14
15	12	15	12	6	11	9	15	13	13	10
16	11	14	16	15	11	13	4	3	12	12
17	13	14	7	14	10	7	13	13	16	12
18	12	17	7	15	11	12	10	13	12	11
19	6	11	13	11	23	9	11	16	13	18
20	21	10	19	7	10	8	11	12	13	12

Table 29. Total yield (number of harvested racemes) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	31	25	33	31	37	25	17	29	31	40
2	35	34	25	31	28	25	29	34	28	41
3	29	35	24	36	16	26	20	25	30	36
4	35	28	44	29	20	20	29	22	33	39
5	34	33	47	33	35	28	21	21	24	47
6	24	30	29	37	27	23	25	24	32	37
7	34	24	29	23	25	31	31	24	26	34
8	33	30	22	34	31	23	15	29	26	45
9	18	25	28	31	24	17	24	24	30	32
10	29	25	20	33	26	20	17	23	29	34
11	33	33	23	32	28	28	28	14	22	40
12	29	24	25	30	31	21	22	24	28	38
13	32	29	27	22	25	19	25	20	33	43
14	23	29	30	25	33	21	9	18	30	26
15	30	26	26	22	26	20	35	25	27	32
16	29	31	38	31	28	26	14	10	25	42
17	32	26	18	28	31	15	23	25	33	35
18	28	34	23	30	30	23	23	24	37	34
19	24	23	29	26	42	17	21	32	30	44
20	44	25	27	30	24	21	26	27	31	31

Table 30. Height of the tallest shoot (cm) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

	Progeny Number									
Replicate	1	2	3	4	5	6	7	8	9	10
1	139	147	140	142	160	119	81	94	158	186
2	159	145	121	151	173	129	127	88	147	135
3	133	153	126	151	97	115	111	102	144	155
4	122	165	161	130	129	120	129	108	137	135
5	146	139	136	142	170	112	115	108	160	142
6	150	123	135	128	138	87	119	108	123	121
7	150	125	128	71	163	105	115	112	127	116
8	120	101	175	164	134	122	129	90	145	119
9	86	156	137	142	133	101	119	100	128	123
10	155	121	193	137	137	123	97	109	132	119
11	138	139	111	140	132	124	125	87	134	152
12	142	104	152	117	103	85	97	98	104	145
13	122	105	112	139	93	100	113	136	133	137
14	147	135	109	160	130	117	109	84	90	110
15	111	117	111	94	131	126	121	108	134	144
16	150	150	149	165	103	115	89	151	124	137
17	123	85	173	109	162	65	104	87	109	122
18	162	119	128	133	143	115	98	120	130	117
19	158	140	185	134	113	96	117	119	89	125
20	112	143	104	130	172	99	123	128	124	108

Table 31. Height of the most recently matured shoot (cm) of inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

	Progeny Number									
Replicate	1	2	3	4	5	6	7	8	9	10
1	117	147	140	142	160	119	-	88	152	73
2	159	132	114	151	173	129	127	83	145	119
3	52	145	126	-	97	115	74	96	144	79
4	110	142	-	73	118	106	103	108	70	135
5	146	107	113	142	62	112	84	69	160	116
6	111	104	96	73	116	74	119	78	72	102
7	150	125	97	70	163	79	103	112	126	91
8	115	101	175	81	134	109	109	72	145	63
9	70	156	108	142	113	59	76	79	93	123
10	150	83	188	137	137	-	97	109	132	95
11	138	139	75	132	132	61	125	87	134	152
12	138	104	152	105	103	67	92	64	96	104
13	122	105	112	139	93	73	113	136	133	131
14	147	-	84	160	130	117	109	84	90	68
15	111	107	77	-	-	-	121	91	134	81
16	103	150	149	103	94	70	69	151	124	113
17	123	77	173	106	162	65	104	74	102	122
18	162	119	128	124	143	115	65	120	107	109
19	149	48	185	132	75	96	117	88	89	108
20	112	143	104	121	172	99	114	128	124	108

Table 32. Mean flower size (cm) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

	Progeny Number									
Replicate	1	2	3	4	5	6	7	8	9	10
1	5.90	6.13	5.13	5.40	6.04	6.27	6.91	6.55	5.92	5.78
2	5.78	5.65	5.33	5.70	5.99	6.95	6.86	5.87	6.00	6.34
3	5.82	6.04	5.27	5.11	5.60	6.21	6.81	7.00	5.97	6.50
4	5.74	6.35	4.98	5.63	5.84	6.34	6.41	6.76	6.19	6.26
5	6.05	5.96	4.94	5.28	5.22	6.75	6.87	6.86	6.18	6.07
6	5.74	5.66	5.11	5.35	5.97	5.99	6.85	6.34	5.98	6.36
7	5.25	6.13	5.18	5.10	6.02	6.66	6.20	7.02	5.76	6.11
8	5.70	6.26	5.20	5.14	5.88	7.11	7.17	6.33	6.20	6.39
9	5.77	5.89	5.29	5.60	5.65	6.87	6.72	6.19	6.09	5.70
10	5.92	6.52	5.46	5.08	5.86	6.67	6.89	6.89	6.32	6.43
11	5.61	5.80	4.82	6.16	5.64	6.53	6.60	7.12	6.00	6.26
12	5.89	6.11	5.22	6.39	5.85	6.60	6.97	6.79	6.41	6.04
13	5.69	5.70	6.03	5.36	5.73	6.48	6.81	6.89	5.68	6.32
14	5.86	6.16	5.12	5.97	5.63	6.70	5.93	6.49	5.82	6.34
15	5.97	6.14	5.03	5.17	5.82	6.48	6.72	6.98	6.07	6.10
16	4.96	6.10	5.41	5.34	5.89	6.94	6.86	6.94	6.14	6.45
17	5.76	6.49	5.52	5.82	5.86	6.89	6.54	6.82	6.24	6.38
18	5.83	6.12	5.04	5.89	5.84	6.74	6.95	7.21	6.16	6.64
19	5.76	6.03	5.35	5.38	5.84	6.56	7.00	6.88	6.30	6.31
20	5.50	5.95	5.34	5.07	5.85	6.42	6.57	6.25	5.97	6.38

Table 33. Mean color ranking of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	3.0	1.8	2.9	3.0	2.0	1.0	1.0	1.0	2.2	1.1
2	2.9	2.1	3.0	2.7	3.0	1.0	1.1	1.0	2.0	1.0
3	3.0	2.0	3.0	3.0	2.0	1.0	1.0	1.0	2.0	1.0
4	3.0	1.9	2.9	2.0	2.0	1.0	1.0	1.1	2.0	1.0
5	3.0	1.9	3.0	2.1	2.8	1.0	1.0	1.0	2.1	1.0
6	3.0	1.9	3.0	2.1	2.9	1.0	1.0	1.0	2.1	1.0
7	3.0	2.0	2.9	2.0	2.0	1.0	1.0	1.0	2.1	1.1
8	3.0	2.0	3.0	3.0	2.9	1.0	1.0	1.1	2.0	1.0
9	2.8	2.0	2.9	2.1	3.0	1.0	1.0	1.0	2.1	1.0
10	3.0	1.8	3.0	2.8	2.0	1.0	1.0	1.0	2.1	1.0
11	3.0	2.0	2.4	2.0	2.1	1.0	1.0	1.0	2.0	1.0
12	2.9	2.0	3.0	3.0	2.0	1.0	1.2	1.0	1.9	1.0
13	3.0	2.0	3.0	1.8	3.0	1.1	1.0	1.0	2.1	1.0
14	3.0	2.2	2.8	2.0	2.1	1.0	1.1	1.0	2.1	1.0
15	3.0	2.0	2.8	2.0	3.0	1.0	1.1	1.0	2.0	1.0
16	3.0	2.0	2.9	2.3	3.0	1.0	1.1	1.0	2.0	1.0
17	2.9	2.2	3.0	3.0	3.0	1.1	1.0	1.0	2.2	1.0
18	3.0	2.1	2.5	1.8	2.9	1.0	1.0	1.0	2.4	1.0
19	3.0	2.0	3.0	3.0	2.1	1.0	1.0	1.0	2.0	1.1
20	2.9	2.0	3.0	3.0	3.0	1.0	1.0	1.0	2.0	1.0

Table 34. Mean scape length (cm) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	18.4	17.8	20.8	19.8	18.7	18.6	17.4	18.0	18.3	18.5
2	16.5	18.2	19.2	17.9	17.2	18.6	15.9	20.1	18.6	21.2
3	17.2	18.0	20.5	20.6	17.5	17.1	18.3	20.1	18.4	21.8
4	17.0	17.9	20.7	16.8	19.0	19.2	19.0	18.4	18.3	20.8
5	18.0	19.4	20.1	20.7	19.8	19.1	17.1	18.2	18.1	21.7
6	17.0	16.4	18.6	21.8	17.6	18.1	20.2	17.3	18.1	21.6
7	19.7	20.0	21.2	20.2	18.1	21.2	18.8	18.8	19.7	23.1
8	16.8	16.4	18.8	19.3	17.6	20.0	17.7	18.9	19.3	20.5
9	17.2	18.1	19.0	17.1	16.6	16.5	19.8	16.6	18.9	20.6
10	14.5	18.4	17.9	20.2	19.4	18.6	18.2	20.8	17.7	22.1
11	17.0	18.0	20.7	18.3	17.2	18.7	19.2	16.4	19.2	21.0
12	18.3	17.7	17.6	16.4	18.8	16.9	19.0	18.2	21.1	18.9
13	18.2	17.9	17.6	21.0	18.9	20.9	19.4	20.4	15.5	22.0
14	15.8	19.0	18.6	16.5	18.7	18.5	18.6	18.0	17.6	20.8
15	17.7	17.3	20.7	22.3	17.3	16.6	17.4	20.9	18.6	23.4
16	12.6	18.6	19.9	21.4	18.6	20.6	19.9	17.7	18.0	23.1
17	16.2	16.6	17.8	15.8	18.6	19.1	19.1	20.1	19.5	22.1
18	17.5	18.1	17.7	16.9	17.5	19.6	20.3	17.2	19.1	23.1
19	16.0	18.5	17.1	17.5	18.1	22.6	16.0	18.9	20.6	22.9
20	18.3	18.6	21.7	19.9	17.1	19.3	17.3	18.2	18.3	22.1

Table 35. Mean raceme length (cm) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	70.4	59.7	73.6	64.7	65.9	61.5	58.8	61.8	71.3	52.2
2	61.7	68.1	62.0	61.5	64.1	63.0	55.2	67.4	65.1	73.5
3	62.4	67.1	73.3	69.6	55.8	59.9	58.6	70.3	62.0	68.0
4	62.9	64.7	62.0	54.7	65.9	63.4	63.0	67.4	63.8	67.9
5	69.2	70.2	65.9	69.6	62.0	66.1	55.6	55.2	66.9	68.7
6	66.6	62.5	57.5	66.8	65.8	56.5	67.8	59.8	60.1	65.9
7	64.8	69.6	73.5	58.6	70.2	66.6	58.1	65.3	61.7	61.9
8	65.3	59.8	60.1	68.5	66.5	66.0	67.4	59.3	69.6	60.5
9	56.5	60.6	66.1	55.3	57.2	52.6	66.8	51.0	68.5	51.6
10	62.9	64.0	60.9	73.3	70.4	57.5	59.3	66.0	63.6	76.6
11	61.0	64.7	57.8	63.0	59.6	57.1	60.5	63.4	70.0	66.1
12	67.7	68.0	60.7	67.5	63.7	63.8	59.0	63.3	63.6	55.8
13	64.6	61.4	61.8	70.7	65.9	62.4	64.2	68.3	55.8	68.9
14	67.2	70.5	61.0	58.1	66.0	62.4	56.8	60.8	62.7	68.6
15	63.8	69.9	69.5	69.1	64.5	55.3	61.0	69.8	66.7	74.5
16	58.0	67.4	61.2	67.0	61.4	72.0	64.7	52.2	61.1	66.8
17	60.1	58.8	60.9	64.8	63.4	68.2	60.3	68.6	67.9	66.5
18	64.2	66.2	63.2	57.9	64.4	65.7	62.3	68.4	64.2	72.0
19	58.9	72.3	64.7	66.6	60.0	71.4	54.0	62.8	64.3	69.2
20	62.5	64.4	78.1	62.8	66.5	62.0	57.9	58.1	61.1	64.9

Table 36. Mean number of initiated flowers per raceme of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	24.3	19.7	24.2	22.1	22.2	18.5	18.2	18.9	25.1	17.8
2	22.1	23.0	20.1	22.5	22.9	18.7	17.1	20.3	21.7	21.5
3	22.1	22.8	22.8	22.4	18.7	19.7	16.9	19.8	21.1	21.3
4	22.7	21.4	20.1	18.6	21.3	19.8	20.5	20.0	20.5	20.3
5	24.4	22.7	20.8	20.2	20.0	21.3	17.8	17.3	22.8	21.8
6	24.1	23.2	18.7	20.9	23.0	17.7	20.4	19.5	20.8	20.1
7	22.3	22.6	24.3	18.5	23.6	19.5	17.7	18.5	20.2	18.3
8	22.8	21.7	20.7	21.9	22.5	19.1	21.1	17.4	22.6	18.3
9	18.8	19.9	21.9	19.9	20.8	15.8	19.9	16.1	22.1	16.2
10	23.1	19.7	18.8	24.5	22.9	17.4	18.7	18.9	20.1	22.8
11	21.8	21.9	18.2	20.8	23.0	16.9	19.0	20.3	23.9	21.7
12	24.0	24.0	20.1	24.4	20.5	20.5	18.1	18.2	18.8	19.7
13	24.3	22.4	20.2	21.0	22.9	17.5	19.0	21.1	22.0	21.4
14	25.6	24.2	19.5	18.4	21.0	18.2	17.0	18.5	23.2	21.6
15	22.0	23.7	23.5	22.0	23.7	14.4	17.9	20.1	22.6	21.2
16	24.0	22.5	18.8	21.8	19.3	20.3	18.9	16.5	21.3	19.2
17	21.5	18.5	20.8	23.4	20.8	18.5	18.0	19.4	22.1	19.5
18	22.9	21.1	21.5	20.4	21.8	19.8	17.7	21.6	20.9	21.7
19	21.5	24.4	23.1	24.0	19.1	22.2	17.1	19.3	19.3	20.5
20	20.8	20.7	25.1	20.1	23.3	17.3	18.6	18.1	19.8	19.3

Table 37. Mean vase life (days) of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	10.6	12.6	13.9	14.2	11.3	12.0	9.3	11.1	12.1	12.1
2	11.7	13.6	11.0	10.8	11.6	10.1	10.8	11.6	10.5	13.6
3	11.3	10.1	14.5	12.9	9.1	10.0	9.3	10.6	11.7	12.6
4	11.5	11.9	13.2	11.4	10.6	11.7	12.1	10.4	11.9	12.4
5	11.3	10.1	14.3	12.4	14.7	10.5	11.3	10.5	9.4	14.0
6	10.1	10.9	13.0	12.5	11.8	11.0	11.0	9.2	10.6	11.6
7	14.2	12.1	12.7	12.9	11.6	11.5	12.8	10.7	10.9	13.1
8	11.2	11.6	12.4	12.5	10.9	11.0	7.8	11.4	12.1	14.6
9	11.8	10.8	12.0	10.5	10.2	9.1	10.7	9.1	9.9	10.0
10	9.9	11.2	11.6	14.6	11.8	11.8	12.9	11.5	13.2	13.5
11	11.5	11.3	13.3	10.8	13.2	11.7	10.3	11.9	10.0	13.1
12	11.1	11.8	11.8	9.6	10.7	11.2	12.0	9.9	9.7	13.1
13	11.9	11.5	10.6	12.7	11.4	11.5	9.6	10.8	10.7	12.7
14	10.1	10.1	11.2	12.1	10.3	9.2	12.9	10.3	11.5	13.8
15	12.0	12.7	13.1	13.1	11.0	8.9	12.6	11.6	11.8	10.9
16	12.1	12.5	14.0	14.1	12.6	11.8	11.8	12.8	11.4	13.2
17	10.8	10.7	10.9	11.5	11.1	8.8	11.4	10.3	11.8	11.6
18	11.5	10.8	12.6	11.7	10.9	9.5	10.7	10.0	10.5	12.8
19	11.4	10.0	12.1	15.3	13.8	9.9	10.5	10.5	10.2	12.4
20	13.7	10.1	13.4	11.7	11.7	9.6	10.4	9.9	10.1	12.5

Table 38. Mean percent bud drop of each plant of the inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Replicate	Progeny Number									
	1	2	3	4	5	6	7	8	9	10
1	2	1	2	1	1	1	1	1	3	2
2	2	0	5	7	1	1	3	3	2	3
3	1	1	2	1	2	3	3	1	1	1
4	3	1	12	3	1	1	2	1	4	0
5	2	2	7	4	7	1	2	1	6	2
6	2	0	7	4	1	2	2	3	2	2
7	1	3	21	9	3	1	0	2	2	2
8	3	1	3	3	3	3	2	3	2	3
9	0	1	1	2	2	0	1	5	2	3
10	0	1	6	7	2	4	1	1	1	1
11	1	2	3	2	0	1	1	2	0	2
12	1	2	5	2	2	0	0	1	1	5
13	1	11	2	2	3	1	0	1	1	1
14	3	2	4	1	3	2	4	2	1	3
15	1	2	8	17	1	2	1	0	2	1
16	6	1	2	2	1	1	1	2	1	1
17	2	1	4	4	1	1	1	1	4	1
18	2	1	3	3	1	2	1	1	2	1
19	6	2	2	3	2	7	1	1	1	1
20	1	2	16	4	2	1	1	1	1	1

Table 39. Analysis of variance of yield (number of harvested racemes) of inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii for several years.

Source	df	1975 Mean Square	1976 Mean Square	1977 Mean Square	1978 Mean Square	Total Yield Mean Square
Progenies	9	2.33**	21.01**	99.62**	31.04**	395.04**
Replicates	19	0.64 n.s.	9.47**	11.96 n.s.	7.07 n.s.	35.67 n.s.
Error	171	0.41	2.65	9.59	9.59	27.33

Table 40. Analysis of variance of height of tallest shoot of inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Source	df	Mean Square
Progenies	9	3047.19**
Replicates	19	525.16 n.s.
Error	171	405.28

Table 41. Analysis of variance of height of the most recently matured shoot of inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Source	df	Mean Square
Progenies	9	3151.92**
Replicates	18	851.31 n.s.
Error	157	756.11

Table 42. Analysis of variance of floral characters of inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Source	df	Flower Size Mean Square	Scape Length Mean Square	Raceme Length Mean Square	Number of Initiated Flowers Mean Square	Vase Life Mean Square	Percent Bud Drop Mean Square
Progenies	9	529.47**	27.70**	48.85*	45.63**	11.96**	40.81**
Replicates	19	9.82 n.s.	2.09 n.s.	24.16 n.s.	2.08 n.s.	2.66**	6.62 n.s.
Error	171	7.26	1.90	24.31	2.84	1.19	5.25

Table 43. Analysis of variance of bench effects on measured characters of inbred and noninbred progenies of D. Jaquelyn Thomas and D. Neo Hawaii.

Source	df	Total Yield Mean Square	Height of Tallest Shoot Mean Square	Flower Size Mean Square	Scape Length Mean Square	Raceme Length Mean Square	Number of Initiated Flowers Mean Square	Vase Life Mean Square	Percent Bud Drop Mean Square
Progenies	3	46.09 n.s.	680.89 n.s.	3.94 n.s.	5.88 n.s.	36.14 n.s.	0.13 n.s.	5.36*	4.77 n.s.
Error	196	44.73	534.05	31.54	3.05	25.24	4.77	1.79	7.02

Table 44. Number of plants and total dry weight of plants of each replicate (flask) of inbred progenies of D. d'albertsii 5 months after transflasking.

Selfing	Generation of Progeny	Replicate 1		Replicate 2		Replicate 3	
		No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)
S1-10 selfed	S_2	46	0.3945	51	0.3344	43	0.2804
K73-1 selfed	S_3	28	0.1095	38	0.1817	47	0.2877
K176-12 selfed	S_4	41	0.3349	50	0.4001	34	0.2055
K176-8 selfed	S_4	43	0.2387	40	0.3343	41	0.2994
K324-20 selfed	S_5	23	0.1326	39	0.3667	35	0.2854
K325-10 selfed	S_5	42	0.2885	38	0.2744	49	0.3984
K324-6 selfed	S_5	48	0.3284	52	0.4530	45	0.3565

Table 45. Number of plants and total dry weight of plants of each replicate (flask) of inbred progenies of D. d'albertsii 10 months after transflasking.

Selfing	Generation of Progeny	Replicate 1A No. of Plants	1A Total Dry Wt. (g)	2A No. of Plants	2A Total Dry Wt. (g)	3A No. of Plants	3A Total Dry Wt. (g)	4A No. of Plants	4A Total Dry Wt. (g)
S1-10 selfed	S_2	32	0.4900	39	0.5475	24	0.3405	36	0.5461
K73-1 selfed	S_3	51	0.6571	31	0.3922	64	0.9571	51	0.8674
K176-12 selfed	S_4	51	0.6949	40	0.8513	48	1.0644	54	1.1218
K176-8 selfed	S_4	70	0.9015	32	0.7168	50	1.1558	24	0.8737
K324-20 selfed	S_5	40	0.3390	32	0.5727	50	0.9468	49	0.8085
K325-10 selfed	S_5	49	0.7316	44	0.6868	52	0.8302	51	0.7612
K324-6 selfed	S_5	45	0.5994	45	0.8566	42	0.7989	53	0.9989

Table 46. Number of plants and total dry weight of plants of each replicate (flask) of inbred progenies of D. schulleri 5 months after transflasking.

Selfing	Generation of Progeny	Replicate 1 No. of Plants	Replicate 1 Total Dry Wt. (g)	Replicate 2 No. of Plants	Replicate 2 Total Dry Wt. (g)	Replicate 3 No. of Plants	Replicate 3 Total Dry Wt. (g)
D159 selfed	S_1	21	0.0522	22	0.0316	36	0.0752
K321-27 selfed	S_2	39	0.0638	48	0.0784	37	0.0633
K321-28 selfed	S_2	38	0.0812	18	0.0219	37	0.1387

Table 47. Number of plants and total dry weight of plants of each replicate (flask) of inbred progenies of D. schulleri 10 months after transflasking.

Selfing	Generation of Progeny	Replicate 1A No. of Plants	Replicate 1A Total Dry Wt. (g)	Replicate 2A No. of Plants	Replicate 2A Total Dry Wt. (g)	Replicate 3A No. of Plants	Replicate 3A Total Dry Wt. (g)
D159 selfed	S_1	25	0.0884	34	0.2851	29	0.1618
K321-27 selfed	S_2	43	0.1287	50	0.3257	53	0.3555
K321-28 selfed	S_2	52	0.1500	39	0.2441	36	0.4520

Table 48. Number of plants and total dry weight of plants of each replicate (flask) of inbred progenies of D. phalaenopsis 'Kosaki'.

Selfing	Generation of Progeny	Replicate 1 No. of Plants	1 Total Dry Wt. (g)	2 No. of Plants	2 Total Dry Wt. (g)	3 No. of Plants	3 Total Dry Wt. (g)	4 No. of Plants	4 Total Dry Wt. (g)	5 No. of Plants	5 Total Dry Wt. (g)	6 No. of Plants	6 Total Dry Wt. (g)
D40 selfed	S_1	49	1.0479	49	1.0660	47	0.9522	42	1.0132	46	0.9804	44	1.0582
K133-1 selfed	S_2	48	1.1290	50	1.3381	51	1.2645	54	1.0896	51	1.3234	53	1.1180
TOl-4 selfed	S_2	55	0.6985	53	0.9523	63	0.7700	55	0.7711	45	0.9245	38	0.6364
TOl-3 selfed	S_2	39	0.5811	43	0.6485	28	0.5000	-	-	-	-	-	-

Table 49. Number of plants and total dry weight of plants of each replicate (flask) of inbred progenies of D. Jaquelyn Thomas 'Y166-1'.

		Replicate											
		1		2		3		4		5		6	
Selfing	Generation of Progeny	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)
Y166-1 selfed	S_1	51	0.2714	54	0.2204	53	0.2854	48	0.2123	45	0.1641	38	0.0990
UH44-50 selfed	S_2	48	0.2158	54	0.3251	54	0.3615	41	0.2820	48	0.3082	55	0.2179
1-6 selfed	S_2	52	0.3886	43	0.4475	40	0.3589	32	0.2089	46	0.2609	47	0.2677
3-1 selfed	S_3	60	0.3317	61	0.3980	75	0.4524	50	0.1978	45	0.2209	46	0.1875
K159-25 selfed	S_3	51	0.2218	49	0.2293	45	0.1329	29	0.0776	44	0.1492	49	0.1260
3-16 selfed	S_3	63	0.4051	65	0.5319	47	0.3977	48	0.2029	60	0.5384	49	0.2173
K159-21 selfed	S_3	43	0.1842	62	0.3860	57	0.2645	45	0.2397	54	0.3579	46	0.1403
K159-19 selfed	S_3	48	0.3144	38	0.1739	50	0.1100	34	0.1685	34	0.2092	37	0.1013
6-14 selfed	S_4	59	0.1644	44	0.1511	39	0.1305	36	0.1200	52	0.2195	38	0.0652
6-10 selfed	S_4	38	0.2675	42	0.3722	44	0.2345	36	0.1821	37	0.2025	44	0.1883
6-12 selfed	S_4	41	0.1984	43	0.2243	33	0.2836	22	0.0642	36	0.1791	22	0.0872

Table 50. Number of plants and total dry weight of plants of each replicate (flask) of inbred progenies of D. Jaquelyn Thomas '2085-4N'.

		Replicate											
		1		2		3		4		5		6	
Selfing	Generation of Progeny	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)	No. of Plants	Total Dry Wt. (g)
2085-4N selfed	S_1	35	0.7726	37	0.8351	43	0.8866	41	0.8314	44	1.0142	42	0.8394
K241-5 selfed	S_2	52	1.0308	50	1.0608	49	0.9568	47	1.1272	52	0.9627	38	0.7746

Table 51. Analysis of variance of plant dry weight of inbred progenies of D. d'albertsii.

Source	5 Months After Transflasking		10 Months After Transflasking	
	df	Mean Square	df	Mean Square
Progenies	6	2.93 n.s.	6	45.53*
Replicates	2	1.96 n.s.	3	60.89*
Error	12	1.46	18	13.93

Table 52. Analysis of variance of plant dry weight of inbred progenies of D. schulleri.

Source	df	Mean Square (5 Months After Transflasking)	Mean Square (10 Months After Transflasking)
Progenies	2	0.38 n.s.	2.74 n.s.
Replicates	2	0.90 n.s.	21.64 n.s.
Error	4	0.51	6.38

Table 53. Analysis of variance of plant dry weight of inbred progenies of D. phalaenopsis 'Kosaki'.

Source	df	Mean Square
Progenies	3	90.12**
Error	17	6.26

Table 54. Analysis of variance of plant dry weight of inbred progenies of D. Jaquelyn Thomas 'Y166-1'.

Source	df	Mean Square
Progenies	10	10.36**
Replicates	5	9.80**
Error	50	1.47

Table 55. Analysis of variance of plant dry weight of inbred progenies of D. Jaquelyn Thomas '2085-4N'.

Source	df	Mean Square
Progenies	1	2.19 n.s.
Replicates	5	1.46 n.s.
Error	5	3.82

LITERATURE CITED

Adair, C. R. and J. W. Jones. 1946. Effect of environment on the characteristics of plants surviving in bulk hybrid populations of rice. J. Amer. Soc. Agron. 38:708-716.

Allard, R. W. and S. K. Jain. 1962. Population studies in predominantly self-pollinated species. II. Analysis of quantitative genetic changes in a bulk-hybrid population of barley. Evolution 16:90-101.

_____, S. K. Jain and P. L. Workman. 1968. The genetics of inbreeding populations. Adv. Genet. 14:55-131.

Balint, A. 1976. Some theoretical problems of inbreeding. Proc. Seventh Cong. EUCARPIA, pp. 41-49.

Belling, J. 1925. The origin of chromosome mutations in Uvularia. J. Genet. 15:245-266.

Bobisud, C. A. 1976. The effects of selection and inbreeding on early yield and flower quality in amphidiploid dendrobium. MS Thesis, Univ. of Hawaii, Honolulu.

Bruce, A. B. 1910. The Mendelian theory of heredity and the augmentation of vigor. Science 32:627-628.

Carson, H. L. 1967. Inbreeding and gene fixation in natural populations. pp. 281-308. In R. A. Brink (ed.) Heritage from Mendel. Univ. Wisc. Press, Madison.

Castle, W. E. 1946. Genes which divide species or produce hybrid vigor. Proc. Nat. Acad. Sci. 32.145-149.

Clausen, R. E. and T. H. Goodspeed. 1925. Interspecific hybridization in Nicotiana. II. A tetraploid glutinosa-tabacum hybrid, an experimental verification of Winge's hypothesis. Genetics 10:278-284.

Collins, G. N. 1921. Dominance and the vigor of first generation hybrids. Amer. Nat. 55:116-133.

Crow, J. R. 1948. Alternative hypothesis of hybrid vigor. Genetics 33:477-487.

Darlington, C. D. 1932. Recent advances in cytology. P. Blakiston's Son, Philadelphia.

Darwin, C. R. 1900. The effects of cross and self fertilisation in the vegetable kingdom. 2nd ed. John Murray, London.

_____. 1904. The various contrivances by which orchids are fertilised by insects. 2nd ed. John Murray, London.

Dobzhansky, T. 1941. Genetics and the origin of species. Columbia Univ. Press, New York.

Dorsman, C. 1976. F_1-hybrids in some out-pollinating crops. Proc. Seventh Cong. EUCARPIA, pp. 197-208.

Duncan, D. B. 1965. A Bayesian approach to multiple comparisons. Technometrics 7:171-222.

East, E. M. 1908. Inbreeding in corn. Rept. Connecticut Agric. Expt. Sta. 1907-1908. Pp. 419-428.

_____. 1909. The distinction between development and heredity in inbreeding. Amer. Nat. 43:173-181.

_____. 1910. A Mendelian interpretation of variation that is apparently continuous. Amer. Nat. 44:65-82.

_____. 1936. Heterosis. Genetics 21:375-397.

_____ and H. K. Hayes. 1912. Heterozygosis in evolution and plant breeding. U.S.D.A. Bur. Plant Indust. Bull. 243.

_____ and D. F. Jones. 1919. Inbreeding and outbreeding. J. B. Lippincott Co., Philadelphia and London.

Frandsen, H. N. and O. Winge. 1932. Brassica napocamestris, a new constant amphidiploid species hybrid. Hereditas 16:212-218.

Goodspeed, T. H. and M. V. Bradley. 1942. Amphidiploidy. Bot. Rev. 8:271-316.

Gorsline, G. W. 1961. Phenotypic epistasis for ten quantitative characters in maize. Crop Sci. 1-55-58.

Haldane, J. B. S. 1936. The amount of heterozygosis to be expected in an approximately pure line. J. Genet. 32:375-391.

Hayes, J. D. and C. A. Foster. 1976. Heterosis in self-pollinating crops, with particular reference to barley. Proc. Seventh Cong. EUCARPIA, pp. 239-256.

Hayman, B. I. and K. Mather. 1953. The progress of inbreeding when homozygotes are at a disadvantage. Heredity 7:165-183.

Hull, F. H. 1945. Recurrent selection for specific combining ability in corn. J. Amer. Soc. Agron. 37:134-145.

Ichijima, K. 1926. Cytological and genetic studies on Fragaria. Genetics 11:590-604.

Imam, A. G. and R. W. Allard. 1965. Population studies in predominantly self-pollinated species. VI. Genetic variability between and within natural populations of wild oats from differing habitats in California. Genetics 51:49-62.

Jain, S. K. and R. W. Allard. 1960. Population studies in predominantly self-pollinated species. I. Evidence for heterozygote advantage in a closed population of barley. Proc. Nat. Acad. Sci. U.S. 46:1371-1377.

Jones, D. F. 1917. Dominance of linked factors as a means of accounting for heterosis. Genetics 2:466-479.

_____. 1918. The effects of inbreeding and crossbreeding upon development. Connecticut Agric. Expt. Sta. Bull. 207.

_____. 1924. The attainment of homozygosity in inbred strains of maize. Genetics 9:405-418.

_____. 1925. Genetics in plant and animal improvement. John Wiley and Sons, Inc., New York.

_____. 1939. Continued inbreeding in maize. Genetics 24:462-473.

_____. 1945. Heterosis resulting from degenerative changes. Genetics 30:527-542.

Kamemoto, H., K. Shindo and K. Kosaki. 1964. Chromosome homology in the Ceratobium, Phalaenanthe, and Latourea sections of the genus Dendrobium. Pac. Sci. 18(1):104-115.

Kannenberg. L. W. and R. W. Allard. 1967. Population studies in predominantly self-pollinated species. VIII. Genetic variability in the Festuca microstachys complex. Evolution 21: 227-240.

Karpechenko, G. D. 1927. The production of polyploid gametes in hybrids. Hereditas 9:349-368.

Keeble, F. and C. Pellew. 1910. The mode of inheritance of stature and time of flowering in peas (Pisum sativum). J. Genet. 1: 47-56.

Konarev, V. G. 1976. Physiological and biomechanical aspects of heterosis. Proc. Seventh Cong. EUCARPIA, pp. 81-93.

Kostoff, D. 1938. Studies on polyploid plants. XXI. Cytogenetic behaviour of the allopolyploid hybrids Nicotiana glauca Grah. X Nicotiana Langsdorffii Weinm. and their evolutionary significance. J. Genet. 37:129-209.

Lindstrom, E. W. 1936. Genetics of polyploidy. Bot. Rev. 2:197-215.

_____ and L. M. Humphrey. 1933. Comparative cyto-genetic studies of tetraploid tomatoes from different origins. Genetics 18: 193-209.

MacKey, J. 1976. Genetic and evolutionary principles of heterosis. Proc. Seventh Cong. EUCARPIA, pp. 17-33.

McDaniel, R. G. and I. V. Sarkissian. 1966. Heterosis: complementation by mitochondria. Science 152:1640-1642.

_____ and _____. 1968. Mitochondrial heterosis in maize. Genetics 59:465-475.

Mok, D. W. S. and S. J. Peloquin. 1975. Three mechanisms of 2n pollen formation in diploid potatoes. Can. J. Genet. Cytol. 17:217-225.

Morely, F. H. W. 1959. Natural selection and variation in plants. Cold Spring Harbor Symp. Quant. Biol. 24:47-56.

Muntzing, A. 1930. Outlines to a genetic monograph of the genus Galeopsis, with special reference to the nature and inheritance of partial sterility. Hereditas 13:185-341.

Newton, W. C. F. and C. Pellew. 1929. Primula kewensis and its derivatives. J. Genet. 20:405-467.

Penny, L. H., W. A. Russell and G. G. Sprague. 1962. Types of gene action in yield heterosis in maize. Crop Sci. 2:341-344.

Poole, C. F. 1931. The interspecific hybrid, Crepis rubra X C. foetida, and some of its derivatives. I. Univ. Calif. Publ. Agr. Sci. 6:169-201.

Quinby, J. R. and R. E. Karper. 1946. Heterosis in sorghum resulting from their heterozygous condition of a single gene that affects duration of growth. Amer. J. Bot. 33:716-721.

Reeve, E. C. R. 1957. Inbreeding with selection and linkage. I. Selfing. Ann. Human Genet. 21:277-288.

Richey, F. D. 1946. Hybrid vigor and corn breeding. J. Amer. Soc. Agron. 38:833-841.

Robertson, F. W. and E. C. R. Reeve. 1952. Heterozygosity, environmental variation and heterosis. Nature (Lond.) 170:286.

Robinson, H. F. and C. C. Cockerham. 1961. Heterosis and inbreeding depression in populations involving two open-pollinated varieties of maize. Crop Sci. 1:68-71.

Sarkissian, I. V. and R. G. McDaniel. 1967. Mitochondrial polymorphism in maize, I. Putative evidence for de novo origin of hybrid-specific mitochondria. Proc. Nat. Acad. Sci. USA 57: 1262-1266.

_____ and H. K. Srivastava. 1969. High efficiency, heterosis, and homoeostasis in mitochondria of wheat. Proc. Nat. Acad. Sci. USA 63:302-309.

Schwartz, D. 1960. Genetic studies on mutant enzymes in maize; synthesis of hybrid enzymes by heterozygotes. Proc. Nat. Acad. Sci. USA 46:1210-1215.

_____ and W. J. Laughner. 1969. A molecular basis for heterosis. Science 166:626-627.

Shull, A. F. 1912. The influence of inbreeding on vigor in Hydatina senta. Biol. Bull. 24:1-13.

Shull, G. H. 1908. The composition of a field of maize. Amer. Breeders' Assoc. Rep. 4:296-301.

_____. 1910. Hybridization methods of corn breeding. Amer. Breeders' Mag. 1:98-107.

_____. 1911. The genotypes of maize. Amer. Nat. 45:234-252.

_____. 1914. Duplicate genes for capsule form in Bursa bursa-pastoris. Zeitschr. f. ind. Abst. u. Vereb. 12:97-149.

_____. 1948. What is "heterosis"? Genetics 33:439-446.

Skovsted, A. 1929. Cytological investigations of the genus Aesculus L., with some observations on Aesculus carnea Willd, a tetrapolid species arisen by hybridization. Hereditas 12:64-70.

Stebbins, G. L. 1957. Self-fertilization and population variability in higher plants. Amer. Nat. 91:337-354.

Suneson, C. A. 1949. Survival of four barley varieties in a mixture. Agron. J. 41:459-461.

Svab, J. 1976. Population-genetic aspects of heterosis maintenance. Proc. Seventh Cong. EUCARPIA, pp. 35-40.

Thompson, J. B. and H. Rees. 1956. Selection for heterozygotes during inbreeding. Nature 177:385-386.

Tysdal, H. N., T. A. Kiesselbach and H. L. Westover. 1942. Alfalfa breeding. Nebraska Agric. Expt. Sta. Res. Bull. 124.

Wright, S. 1921. Systems of mating. II. The effects of inbreeding on the genetic composition of a population. Genetics 6:124-143.

_____. 1922. Coefficients of inbreeding and relationship. Amer. Nat. 56:330-338.

Yarnell, S. H. 1931. A study of certain polyploid and aneuploid forms in Fragaria. Genetics 16:455-489.

Zirkle, C. 1952. Early ideas on inbreeding and crossbreeding. In Gowen, J. W. (ed.), Heterosis. Iowa State College Press, Ames, Iowa.