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QUANTITATIVE INHERITANCE OF LEAF SHAPE
CHARACTERS IN TOBACCO
(Nicotiana tabacum L.)

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ABSTRACT

An F_1 half diallel cross experiment with 8 parents (i.e. $\frac{1}{2} p (p + 1)$ combinations) was used to study the quantitative inheritance of leaf shape characters in tobacco (Nicotiana tabacum L.). The effect of stalk positions on the inheritance of these characters was also included. The study was carried out under a glasshouse conditions. The parental lines used in the crosses represent a random sample of leaf shape characters available in New Zealand germplasm collection.

Except for wing area (2nd leaf), phenotypic analysis showed that there was a high genetic variability for other characters.

The genetic analysis of the diallel indicated that inter-locus interaction (epistasis) was of little importance for most of the characters studied. Additive genetic variance was the main component of the total genetic variance. Heritability estimates ranged from moderate (approximately 40 %) to moderately high (approximately 70 %) for most characters. Near similar values were obtained from both the narrow and broad-sense heritability estimates. Very little hybrid vigour was observed for both leaf area and leaf dry weight.

Both the phenotypic and genotypic correlation coefficients between selected pairs of characters were in good agreement with each other in terms of direction and levels of significance. The estimates were generally high and highly significant.

The components of genetic variance (i.e. additive and dominance genetic variance), heritability and correlation coefficient estimates were generally larger in the middle as compared to the top or bottom leaves.

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1. INTRODUCTION

The genus Nicotiana, which has about sixty four, recognised species is a member of family Solanaceae (Smith, 1968, 1974). Of these species, tobacco, Nicotiana tabacum L. is the only species which is commercially grown and has never been found wild (Goodspeed, 1954). Tobacco is far the most important in modern agriculture and international trade as compared to other Nicotiana species.

Tobacco is the most widely grown non-food crop where only its leaves are of commercial value (Akehurst, 1981). As a result, much attention has been given to leaf characters. The total leaf area per plant is always high even though the leaf size varies from one cultivar to another. The individual leaf area depends on its position on the stalk of the plant. The plant is generally pyramidal in shape with the biggest leaf just above the ground (Lapham, 1975). As quoted by Garner (1946), a favourably grown tobacco leaf of many cultivars in America ranged from 93 to 139 cm² in area. A plant which has about 18 leaves therefore would produce a total area of about 1.7 m² to 2.5 m². Went (1957) has shown that the top : root ratio of tobacco is higher than any other cultivated species.

The economic yield and quality of the crop are determined by: the number and size of harvestible leaves, thickness and uniformity of the lamina, various other leaf shape characters and several biochemical factors. Leaf shape is important since it will determine the ratio

of lamina-to-midrib and lamina-to-vein. A measure of leaf area is also essential since it would be useful as an index of growth for the intermediate stages in agronomical and physiological studies (Hunt, 1978). An estimate of leaf area per hectare will aid in the correct application of fungicides and insecticides. Other characters such as the presence of auricles, petioles and characteristics of the veins are also important traditionally. Some of these characters have been used by some breeders as criteria of evaluation (Jones and Collins, 1959) and to characterise cultivars (Van der Veen, 1957; Van der Veen and Bink, 1961; Humphrey et al., 1965; Gordon, 1967, 1969; Eugechi, 1971, 1972).

Leaf shape ranges from very broad to very narrow, at both the lamina and the petiole wing. Leaves may have petioles or be sessile; auricles may be present or absent; lamina may be flat or bubbled; and vein-angles may be acute or obtuse.

Qualitative genetics of these leaf shape characters have been studied widely (Van der Veen, 1957; Van der Veen and Bink, 1961; Humphrey et al., 1965; Gordon, 1969; Eugechi, 1971, 1972). It has been shown that three major pairs of alleles (Pdpd, Ptpt and Brbr) affect leaf width, wing width, petiole length and size of auricle. The dominant genes Pd and Pt cause a longer petiole, narrower wing, narrower leaf blade and a more acute angle of veination as compared to the recessive pt and pd genes. Brbr, on the otherhand, affects wing width to a relatively large extent but was found to have insignificant effect on the other characters. The BrBr genotypes have petioles

(no wing) and brbr were sessiled (winged). With these three major pairs of alleles in combination, a range of leaf shape phenotypes can be obtained. The expression of these phenotypes was also affected by their stalk positions.

Of these characters, only leaf width and length have been studied quantitatively. It has been shown that additive genetic variance was the main variance component for these characters. However, the quantitative inheritance of other leaf shape characters such as wing width, petiole length, auricle area and characteristics of the veins has not been studied. This is of particular interest with respect to the range of genotypes and environments found in New Zealand.

This project was carried out to study the quantitative inheritance of these leaf shape characters using cultivars potentially of use in New Zealand. The effect of leaf positions, that is 'lug', 'cutter', 'leaf', and 'tip' on the quantitative inheritance of these characters was also examined.

2. REVIEW OF LITERATURE

2.1 LEAF SHAPE CHARACTERS IN TOBACCO

2.1.1 Variations of leaf shape characters.

There are a range of cultivars available and they have different types of leaf shape characteristics. Some of the leaf shape characteristics which are distinct amongst these cultivars are: the shape and size of the wing; the length of the petiole; the shape of the lamina; the shape and size of the auricle and sinus; characteristics of the vein; and the characteristics of the lamina and its margin.

By using these characteristics, Van der Veen (1957) showed that the materials he studied had a range of leaf shape characteristics. The wing ranged from very narrow to very wide in combination with a range of petiole lengths. Some of these genotypes were also found to have stem-clasping auricles but not in the others. The angle of veinations ranged from very wide (75° - 80°) to acute (55° - 60°). Based on the definitions proposed by Willis (1960), the shape of the lamina ranged from ovate - orbicular (length: width ratio about 1.5) as in Hongaars Gartenblatt and Atropurpurea to lanceolate (length : width ratio about 3.0 to 3.5) as in Keurhost Elite. Such variations in some of these leaf shape characters were also shown by Datta and Mukherjee (1974) and Mukherjee (1974).

These leaf shape characters were also used by some other workers to describe the range of genotypes used in their studies (Van der Veen, 1957; Van der Veen and Bink, 1961; Chaudhry and Munshi, 1962; Humphrey et al.,

1965; Povilaitis, 1967; Eugechi, 1971). It was shown that the genotypes described by them were homozygous for these leaf shape characters. With three major gene pairs (Ptpt, Pdpd, and Brbr) in combinations (Van der Veen, 1957; Van der Veen and Bink, 1961; Humphrey et al., 1965; Eugechi, 1971, 1972), twenty seven possible genotypes with a range of leaf shape characters would be produced when they were crossed with each other.

Besides those described, other leaf shape characters such as curvature of the tip, the thickness and smoothness of the lamina (or wrinkleness between the lateral veins), marginal sagging, rolling and curling of the leaf and the type of leaf margin were also reported (Kadam and Murty, 1958; Mann and Matzinger, 1965; Silber and Burk, 1965; Gordon, 1969; Lakshminarayana et al., 1971; Qazi and Khan, 1971; Lamprecht, 1979).

In addition to the variations due to genotypes, some of these characters such as leaf shape, leaf thickness, trichome density and marginal sagging also varied to a certain extent with their stalk positions and the environments in which they were grown. It has been shown that leaves are thicker (Barnard, 1960; Burk et al., 1971; Tso and Chaplin, 1977), narrower leaf blades (Sastry and Gopinath, 1968) and higher trichome numbers (Burk et al., 1971; Tso and Chaplin, 1977) in the upper as compared to the lower stalk positions. Raper and Thomas (1972) and Raper (1973) showed that the leaf shape (length/width) were higher in the plants that were grown under day/night temperature of 22°/18° C as compared to those under 18°/14° C temperature regimes.

2.1.2 Main laminar shape measurements

Willis (1960) defined leaf shape as the ratio of leaf length (L) to width (W). Based on this, the leaves having the ratio of about 3.0, 2.5 and 1.5 were referred as lanceolate, lanceolate-ovate, and ovate-orbicular respectively. Due to its simplicity, this approach has been used by many tobacco breeders to measure leaf shape (Van der Veen, 1957; Van der Veen and Bink, 1961; Chaudhry and Munshi, 1962; Povilaitis, 1965; Sastry and Gopinath, 1968). Eugechi (1971) however, used the ratio of leaf width to length.

Raper et al. (1974) also defined leaf shapes as L/L_I and W/W_b , where L = length of the midrib, L_I = the distance along the midrib from the base of the petiole to the intercept of the axis of maximum width, W = leaf width at widest section and W_b = width across the base of winged petiole.

2.1.2.1 Curve fitting - an approach to leaf-shape estimation

The use of curve fitting as an approach to plant growth analysis has been used by many researchers (Vernon and Allison, 1963; Allison and Watson, 1966; Hughes and Freeman, 1967; Kirby, 1969). In this approach, a regression curve was initially fitted to describe the change of one variable with respect to another. As an example, Vernon and Allison (1963) showed that yield (y) changed with time (x) following a second order polynomials (quadratic curves)

$$\text{i.e. } y = \hat{b}_0 + \hat{b}_1x + \hat{b}_2x^2$$

where y = yield, x = time, and $\hat{b}_0$, and $\hat{b}_1$ and $\hat{b}_2$ are constants.

As shown by Causton (1977), by differentiating the above equation with respect to x , a new function of x that is

$$\frac{dy}{dx} = \hat{b}_1 + 2\hat{b}_2x$$

was obtained. This new function (i.e. $\hat{b}_1 + 2\hat{b}_2x$) which is also known as first differential coefficient is the rate of change of y with respect to x . Thus, this is the gradient of the curve at particular point x . The second differential coefficient (i.e. $2\hat{b}_2$) will then give the rate of change of gradient. By using the example given by Vernon and Allison (1963), the first differential coefficient can be physically interpreted as growth rate and the second differential equation as rate of growth rate.

The same principle can also be used to estimate leaf shape. This can be done by fitting a regression curve to relate the change of leaf margin positions (i.e. distances from the midrib to the leaf margin with respect to midrib positions (i.e. distances along the midrib from a datum). The first differential coefficient of this fitted regression curve will then give the rate of change of margin positions with respect to midrib positions. Consequently, the second differential coefficient is the rate of change of the change of margin positions. This coefficient can thus be used as an index of leaf shape.

2.2 LEAF SHAPE CHARACTERS AND THE VALUE OF THE CROP.

The value of the crop is the product of its yield and quality. In either flue-cured, dark fire-cured, light air-cured (including Burley and Maryland), dark air-cured or Oriental tobacco, both yield and quality

were affected by various leaf shape characters. For example, the uniformity of the laminar surface, percentage dry weight of midribs, the presence of auricles are some of the leaf shape characters that directly determine the actual usable yield. This is true either by reducing the actual laminar area for manufacturing purposes or by increasing the damage done during the physical handling of these leaves. For example, the narrow leaf which has a higher percentage of the midrib is less desirable as compared to the broader type leaf. This is because for manufacturing purposes, either all or a portion of the midribs are removed and discarded. A positive relationship between leaf shape (length/width) and percentage of midrib proportion was shown by Chaudhry et al. (1969). Sastry and Gopinath (1968) showed that the higher proportion of midrib to laminar weight was due to the leaf length and thus they suggested that the actual laminar weight may be increased by improving the leaf width rather than the leaf length. According to Robinson et al. (1954), leaf width can be easily improved. Longer leaf might also be responsible for leaf breakages during harvesting and tying of the leaf to the stick for curing.

The length and width of the leaf are another two factors which are related to the yield. Several workers have shown that the product of leaf length and leaf width was highly correlated with the leaf area and thus the yield potential of the plant. These relationships were then used to establish equations to convert the leaf length (L) and width (W) to leaf area (A). Tejwani,

et al. (1957) suggested that $A = 0.60 (L + W) + 4.2$ and $A = 0.66 (L \times W) + 0.2$ for leaves greater and smaller than 2581 cm^2 respectively. Suggs et al. (1960), working with four varieties, two spacings and eight moisture levels suggested that $A = 0.6345 (L \times W)$ with very little effect for variety and moisture level. Coefficient of 0.7028 was suggested for small leaves. By studying Type 41 Pennsylvania broad leaf tobacco, McKee and Yocum (1970) suggested that coefficient of 0.664 for leaves of Pennleaf 1, 0.648 for Swarr-Hibshman and 0.612 for Pennbel 69 should be used. It seems that these results were comparable with each other. However they also showed that the value of the coefficients depend on leaf size, stalk positions and genotypes.

Raper et al. (1974) then established a single relationship by which the variations due to stalk position and genotypes can be accommodated. The relationships suggested by them was $A = 0.6639 (1 + 0.3803 (1.31 - (L/L_I)^{0.33}) + 0.1784 (2.19 - (W/W_b)^{0.50}) L \times W$, where L_I is the distance along the midrib from the base of the petiole to the intercept of the axis of maximum width and W_b is the width across the base of winged petiole. The L/L_I was used to cooperate the variations due to temperature-environments while W/W_b was for the variations due to genotypes and stalk positions.

A significant association between stem diameter and leaf area was also reported (Splinter and Beeman, 1968). They showed that the leaf area (A) is related to the stem diameter (D) as follows: $A = 2620 D^{2.726}$ with R^2 (coefficient of discriminant) = 0.995 for growth cabinet plants

and $A = 2148 D^{2.863}$ with $R^2 = 0.986$ for field plants.

These relationships however hold only up to the initiation of the flowering stage.

This leaf area can then be used to estimate the leaf dry matter yield (Matar, 1978). He suggested that LDW (leaf dry weight) = $0.0062A + 1.03$. Leaf area is also useful for agronomical and physiological studies such as growth analysis and estimating photosynthetic ability of the plant (Hunt, 1978). Leaf area as an aid in determining an optimum application rate for fungicides and insecticides can also be useful.

Leaf shape characters are also related to the quality of the crop and one good example is the characteristics of the veins (Abdullah, 1970). Generally speaking the manufacturers prefer fine veins. This is especially so for smoking and chewing tobaccos. The thickness of the leaf which is another factor determining the quality of the leaf is closely related to the characteristics of the veins. For Burley types, Lapham (1975) also showed that thin leaves were easily spoiled during harvesting, curing and grading.

The quality of tobacco leaf is also affected by the density of trichomes (glandular hairs) since the glandular materials excreted by these hairs are the primary source of aroma (Abdullah, 1970; Akehurst, 1981). In Oriental tobacco, trichome density is correlated to the size of the leaf (Wolf, 1962). Leaf size is also important in cigar wrapper leaf since it determines the number of cigars wrapped with minimum wastage.

Burk and Chaplin (1968) discussed the importance of some leaf shape characters in relation to mechanical harvesting in tobacco. According to them, the leaf which had a small leaf length to width ratio (i.e. a rounded leaf) was more adaptable to mechanical harvesting than the one with bigger leaf length to width ratio (i.e. a long and narrow leaf). This is mainly due to the fact that the broad and rounded leaf has less tendency to droop at the tip and thus less interference with the harvesting as compared to the long and narrow leaf. The uniformity of the leaf size and shape across the stalk positions is another important factor in relation to mechanical harvesting (Chaplin, 1978).

In addition to those described, characters such as leaf shape, petiole length, width of wing and auricle area are also important traditionally. Plants with wide leaf, short petiole, wide wing width and large auricle are usually accepted as an ideotype.

2.3 QUALITATIVE ANALYSIS OF LEAF SHAPE CHARACTERS IN TOBACCO

As cited by Van der Veen (1957), Howard (1913) was the first to make a systematic study on the inheritance of leaf shape characters in tobacco. By studying the petiole characteristics in various crosses of F_1 , F_2 , and F_3 generations, she postulated that there were two factor pairs for indentation.

Since then, many workers in the field of N. tabacum genetics have focused their attention on the petioled versus sessile alternatives, which were correctly

interpreted by most of them as simple Mendelian segregations, that is, one locus two allele type of inheritance (Honing, 1939; Clausen and Cameron, 1944; Kadam and Radhakrishnamurthy, 1953). Later studies were then carried out on other leaf characters such as leaf length, leaf width, the presence of auricles, types of laminar margin and angle of veinations. Of all these, Van der Veen (1957)'s observations were the most significant. By using four distinct phenotypes and crossing them in all possible combinations, the data obtained from F_2 , F_3 and backcrosses generations indicated that the leaf type depends mainly on three factor pairs. These three factors were directly comparable to those of Clausen and Cameron (1944) and he named these Ptpt, Pdpd, and Brbr. Ptpt and Pdpd had pleiotropic and cumulative effects upon petiole length, width of wing, width of lamina, and angle of veination. The dominant genes at loci Pt and Pd caused a longer petiole, narrower wing, narrower width, and a more acute angle of veinations as compared to the recessive pt and pd genes. Brbr affected wing width to relatively large extent but not on other characters. Leaves of Brbr type were found to be sessiled and brbr were petioled.

In a later study, Van der Veen and Bink (1961) showed that Ptpt and Pdpd also had a pleiotropic effect on other characters such as leaf number, rate of leaf production at young stage and internode patterns. It was shown that Pt and Pd increased the total number of leaves, caused the internodes shorter and reduced the development of laminar tissues of the leaf base.

On recent cultivars, most studies were based on Hicks varieties. Humphrey et al. (1965) showed that there were two loci responsible for the inheritance of leaf shape characters, which they named Aa and Bb. The effect of Aa was found to be twice as much as that of Bb. Therefore, it seemed to agree with the Ptpt and Pdpd factors discussed by Van der Veen (1957) and Van der Veen and Bink (1961). Similar observations were also reported by Eugechi (1971).

Gordon (1969) studied Hamilton Hicks which had unusually broad leaf, with marginal sagging and he had suggested that this phenotype could be due to another allele at Pdpd or Ptpt locus. However it was possible also that the Hamilton locus was a totally new one.

The inheritance of other leaf shape characters such as the curvature of the tip, leaf curl, wrinkleness and rolling of the leaf were also reported. Curved leaf tip was found to be inherited as single recessive gene (Kadam and Murty, 1958), whereas curled leaf lamina found in Burley tobacco was due to partially dominant genes (Silber and Burk, 1965). Mann and Matzinger (1956) suggested that wrinkled leaf was inherited as single dominant genes. They also showed that the wrinkled leaf phenotypes were higher in yield than the normal lines. However, these wrinkled phenotypes are of little practical use since they have very low quality. Leaf roll abnormality was determined by single recessive genes (Wolf, 1960; Lamprecht, 1979).

2.4 QUANTITATIVE ANALYSIS OF LEAF SHAPE CHARACTERS IN TOBACCO

2.4.1 The concept of quantitative genetics in plant breeding.

According to Falconer (1981), "quantitative genetic is concerned with the inheritance of those differences between individuals that are of degree rather than kind." Thus the variations in quantitative traits form a continuous array of values from one extreme to another as in contrast to that of qualitative traits in which variations are characterised into discrete classes. Basically, the extension of qualitative to quantitative genetics can be made by extending the concept of: (1) 'single progeny' to 'populations' which consists of a large group of individuals and progenies and, (2) the 'classification' of discrete classes to 'measurement' of continuous variations. Based on these propositions, qualitative traits can also be studied quantitatively.

The manipulations of the genetic variations in these quantitative traits are the most important aspect of quantitative genetics in any plant breeding programme. This can be achieved by inbreeding, hybridisation, and selection. However, before any progress can be achieved, the consequences of such manipulations have to be well understood. This is the basis of most quantitative research studies. The concepts and applications of such studies to the plant breeder have been reviewed by Sprague (1966); Moll and Stuber (1974), Mather and Jinks (1971, 1977); Jinks (1979) and Falconer (1981). They

generally showed that concepts such as variance component estimate, inbreeding depression and heterosis, genotype-environment interaction, response to selection, and heritability are very important to the plant breeder since they have direct bearing on the consequences of any specified plan of breeding.

Evaluations of inheritance in quantitative genetic research studies depend on the valid estimate of the respective genetic variances. These estimates are however based on the measurement of the phenotypes, and hence are based on the estimate of phenotypic variance. From here, the relationship between the components of genetic and phenotypic variance and covariance can be determined.

2.4.2 Analysis of variance.

For significance testing, and estimation of the components of variance, the analysis of variance method is commonly used. Thus the experimental data obtained must conform to the basic assumptions required in the development of this technique. If the data do not conform to these assumptions, such analysis may cause a researcher to make conclusions that are not justified. He may also overlook important conclusions that would be reached if the data were properly analysed. The assumptions upon which analysis of variance is based are briefly as follows (Cochran, 1947; Eisenhart, 1947):

- (i) Independence distribution of error variance,
- (ii) Normal distribution of error variance,
- (iii) Homogeneity of error variance across subsets of data

and (iv) Additivity of treatments and environmental effects.

In practice however, we can never be certain that all the assumptions hold with a particular set of data and often there are reasons to believe that some are false. Detailed discussions on the consequences where these assumptions were not valid and suggestions for remedial procedures to be carried out were given by Eisenhart (1947), Cochran (1947) and Bartlett (1947). In the case of non-normality of error variance for example, the true level of significance is usually greater than the apparent level. Fortunately however, the deviation does not affect the validity of assumption too seriously. The dependent distribution of error variance can also mislead the levels of significance. The best insurance against seriously violating these two assumptions (assumptions (i) and (ii)) is to carry out an appropriate randomisation for the particular experimental design used. The heterogeneity of the error variance on the otherhand can be corrected by several ways. Firstly, seperating data into groups such that the error variance for each group is homogeneous. These sets of data were then analysed separately. Secondly, by weighting the mean according to their variance and thirdly, by transforming the data in such way that the error variance will be homogeneous. In the case of non-additivity of treatment effects such as multiplicative, again transformations are available ti change the data to fit the additivity model (assumption iv).

However, for most biological data, it is well accepted

that the disturbances resulting from the failure of the data to satisfy these assumptions do not invalidate the procedure (Cochran and Cox, 1957; Steel and Torrie, 1980). Thus, the procedures for testing the hypothesis and estimating confidence intervals should be considered as approximate, not exact (Steel and Torrie, 1980).

2.4.3 Estimation of genetical variance

To understand the mode of inheritance of each character under study is the basic principle required in any breeding programme. This can be achieved by the estimation of genotypic and phenotypic variances involved.

Although in earlier years, apparent variability, (i.e. the variability due to the phenotypic effect) was the main form of variability studied, methods are available to partition this variability into the environmental and genetic effects. In addition, estimates on the type of gene action (i.e. dominance and additive effects) can also be obtained. This information has direct bearing on the kind of breeding programme to be followed. If the additive genetic variance is the main variance component for example, breeding procedures by which these additive genes can be utilised such as pedigree breeding should be used. On the otherhand, in the presence of high proportion of dominance genetic variance, hybrid or synthetic variety breeding might be useful. Some of these procedures were discussed by Allard (1960); Simmonds (1979) and Poehlman (1979).

Generally, there are two basic approaches by which the components of genetic variance can be estimated, namely:

analysis of mean (Jinks, 1956; Hayman, 1958, 1960b) and analysis of variance (Hayman, 1954; Jinks, 1954; Hayman and Mather, 1955; Griffing, 1956). As shown by Hayman (1958), extra information on the three kinds of epistatic variance that is the interaction between additive effects, between additive and dominance effects and between dominance effects can be obtained from the analysis of means as compared to the analysis of variance approach. However, he also pointed out that the simplest experiment required two inbred lines, their F_1 , F_2 , and first backcross generations. Thus, generation mean analysis not only takes more time but also limits the number of parents that can be sampled for use in the breeding programmes. However, in the absence of epistasis, information on the dominance and additive genetic variances can be obtained only in one generation from the analysis of variance approach.

In the analysis of variance approach, again, there are various designs available. For all these designs, basically relatives are developed by some system of mating and grown in a set of environments. A least square analysis of these observations leads to the estimation of the components of variance and covariance in which they can be genetically and environmentally interpreted. These utilises either the analysis of variance, covariance or regression techniques. Detailed descriptions of these mating designs were given by Cockerham (1963). Of these designs, diallel mating is the one which is commonly used in plant breeding programmes due to its simplicity.

2.4.4 Diallel analysis: Theory and applications

Diallel mating design can be defined as a set of all possible crosses amongst a random group of parents, with or without inclusion of the reciprocal crosses and selfed parents.

Based on this definition, diallel analysis can be classified as follows (Hinkelmann, 1976):

- (i) diallel mating type I. In this design, each member of a group of parents used paternally are mated to each other of another group of parents used maternally. This design is referred to as factorial mating design by Cockerham (1963) or mating design II of Comstock and Robinson (1948, 1952).
- (ii) diallel mating type II. This mating design involves all possible crosses of a set of inbred parents (Hayman, 1954; Jinks, 1954; Griffing, 1956, Kempthorne, 1956; Mather and Jinks, 1971, 1977).
- (iii) partial diallel cross of type I and type II. In this design, all possible matings do not need to be made as in (i) and (ii) (Kempthorne and Curnow, 1961; Fyfe and Gilbert, 1963; Dhillon and Singh, 1979).
- (iv) two level diallel crosses (Hinkelmann, 1974). This design consists of crosses both at the population and individual level. This can also be considered as composite of two diallel crosses: that is type I (crosses at population level) and type II (crosses at individual level within each group).

(v) variations of the pure forms described above.

This includes top cross by which a common parent is used to mate with each member of another group of parents (variation of type (iii)). Another example is nested mating design in which a group of parent used paternally (maternally) is mated to a different group of parents used maternally (paternally). This is a variation of (ii) and is also known as mating design I of Comstock and Robinson (Comstock and Robinson, 1948, 1952).

Of these designs, diallel mating type II is widely used in plant breeding programmes. In most literatures, this design is referred to simply as diallel mating design. When dealing with multi-cross experiments, this design can be extended to three-way (Rawlings and Cockherham, 1962a) and four-way (Rawlings and Cockherham, 1962b) mating designs. These designs involved all possible matings of either three or four groups of parents.

Depending on whether the reciprocals or self-parents are included or not, generally there are four different types of diallel crosses (Griffing, 1956):

- (i) parents, one set of F_1 's and reciprocals are included (i.e. all p^2 combinations where p is the number of parents);
- (ii) parents and only one set of F_1 's (i.e. $p(p + 1)$ combinations);
- (iii) one set of F_1 's and reciprocals F_1 's but not the parents (i.e. $p(p - 1)$ combinations);
- (iv) only one set of F_1 's but neither parents nor

reciprocals are included (i.e. $\frac{1}{2} (p - 1)$ combinations).

Depending on the type of information to be obtained, the plant breeder should make a choice between these types of crosses.

All the designs briefly mentioned are based upon the following basic genetic assumptions (Hayman, 1954):

- (i) diploid segregation
- (ii) no difference between reciprocal crosses (i.e. no maternal or cytoplasmic effects)
- (iii) independent action of non-allelic genes (no epistasis)
- (iv) homozygous parents
- (v) genes are independently distributed between the parents

and (vi) no multiple allelism (i.e. 2 alleles per locus).

Under certain experimental conditions, models are available in which one or more of these assumptions are satisfied. For example, assumptions (i), (ii) and (iv) satisfy many genetical systems and others are only useful simplifications (assumptions (iii), (v) and (vi)).

However, the effects of some of these assumptions are less on the analysis as compared to the others. As an example various researchers had shown that the additive epistatic effects (assumption (iii)) did not alter the relative importance of additive and dominance variance estimates significantly (Matzinger et al., 1960, 1966, 1972; Matzinger, 1968; Legg and Collins, 1971a, 1971b, 1975). Assumption (v) is satisfied in cases where the population of inference can be assumed to be random.

Diallel analysis was first described by Yates (1947)

and since then three main approaches are evident in the treatment of diallel cross data. These are the methods of: (a) Kempthorne (1956), (b) Griffing (1956) and (c) Jinks-Hayman (Hayman, 1954; Mather and Jinks, 1971, 1977). These main approaches differ in three main ways namely: the ultimate population under investigation, genetical informations that can be obtained, and methods of estimation.

In Kempthorne's approach, the genetic components of variation are estimated by assuming that the parents used in the crosses are a random sample from a random-mating population. In Griffing's approach, the analysis is based only on F_1 families, from which the additive and non-additive genetic variances are obtained in terms of general and specific combining abilities. Griffing (1956) pointed out that the parents used for his approach can either be a fixed, or a random sample of inference population. The two methods of analysis from this dichotomy of approach were discussed. The terms specific combining ability (sca) and general combining ability (gca) are related to the components of genetic variance as follows (Kempthorne, 1955; Griffing, 1956):

$$\sigma^2_A = 2\sigma^2_{gca}$$

$$\sigma^2_{NA} = \sigma^2_{sca}$$

where σ^2_A is additive genetic variance, σ^2_{gca} is general combining ability variance, σ^2_{NA} is non-additive genetic variance and σ^2_{sca} is specific combining ability variance. However, this relationship hold true only in the absence of epistasis, and the parents are fully inbred (Falconer, 1981).

In contrast, however, Jinks-Hayman's methods of analyses estimate the genetic situations in a set of lines

in terms of four different components of genetic variance namely:

- (i) $\hat{D}$ - component of variation arising from the weighted sum of d^2 ($= 4 \sum UVd^2$), that is, the additive effect of genes;
- (ii) $\hat{H}_1$ - component of variation arising from the weighted sum of h^2 ($= 4 \sum UVh^2$), that is, the dominance effects of genes;
- (iii) $\hat{H}_2$ - component of variation arising from the h increment of all genes ($= 16 \sum U^2 V^2 h^2$), that is, dominance indicating the symmetry of positive and negative effects of genes;
- (iv) $\hat{F}$ - an indicator of the relative frequencies of dominant and recessive genes ($= 8 \sum UV \cdot (U - V) dh$), that is, the covariation of additive and dominance effects.

These estimates are based on the proposition that at any one locus A-a, the effects of three possible genotypes AA, Aa and aa are represented by da, ha, and -da respectively. The deviations from the mid-parent value, m are used to express these effects. The frequencies of the alleles A and a are assumed to be Ua and Va respectively.

Jinks-Hayman's approach was initially developed based on the fixed set of inbred lines (Hayman, 1954). However, Hayman (1960a) extended the model from a fixed set of inbred lines to the sampled inbred lines.

Some basic genetical information can also be established if we regress W_r (array-offspring covariance) on V_r (array variance) (Hayman, 1954; Jinks, 1954; Mather and Jinks, 1971, 1977). This (W_r , V_r) graph can be

interpreted in terms of:

- (a) the type of dominance (the point where the line cuts the W_r axis);
- (b) the relative proportion of dominant to recessive genes in the parents (the position of (W_r, V_r) points along the line); and
- (c) the presence of interlocus interaction (significant deviation of regression line from a slope of one).

However, such interpretations are statistically valid only when (W_r, V_r) regression has an acceptable R^2 (coefficient of determination) value. Low R^2 indicates that a high proportion of variations due to V_r are not explained by W_r .

The model used in Jinks-Hayman's analysis assumes that there is no epistasis. Two solutions were proposed when any set of data did not follow the additive-dominance model (Hayman, 1954), that is, by either rescaling the data or by removing (adjusting) the interacting lines or crosses (Hayman, 1954).

As other mating designs, diallel mating designs were used to obtain information on the genetic system of the characters studied. Once this information is obtained, the plant breeder will be able to decide the most effective breeding programme to follow (see section 2.4.3). However, there are some practical limitations related to it. These are mainly of two types: that is, the difficulty in getting hybrids, and the limitations of experimental resources available. For such reasons, less study of this type has been done in cereals, for example as compared to maize or tobacco where the F_1 hybrids can

be easily obtained in large numbers.

2.4.5 Diallel analysis of leaf characters in tobacco.

For the last two decades, diallel mating designs have been widely used in genetical and plant breeding studies in tobacco. These studies were based either on flue-cured tobacco (Matzinger et al., 1960, 1962; Murty et al., 1962; Lamprecht, 1964; Gopinath et al., 1966; Chaplin, 1966, 1967; Povilaitis, 1966, Lamprecht and Botha, 1975), Burley and Maryland types (Legg et al., 1970; Matzinger et al., 1971, Lamprecht, 1973; Fan and Aycock, 1974), cigar tobacco (Dubey, 1976a, 1978; Ogilvie and Kozumplik, 1980) or combination of different types (Povilaitis, 1970, 1971; Vanderberg and Matzinger, 1970). These studies were conducted on characters such as disease resistance, growth characters, and yield components. Generally, it is observed that the main component of the genetic variance for the quantitative characters in tobacco is additive genetic variance. The same trend was observed for leaf size characters such as leaf length and leaf width (Matzinger et al., 1960; Lamprecht, 1964; Povilaitis, 1967; Dubey, 1978; Ogilvie and Kozumplik, 1980). Similar results were also obtained when other mating designs such as generation means analysis of Hayman (Povilaitis, 1964; Oupadisakoon and Wernsman, 1977) and mating design I of Comstock and Robinson (Robinson et al., 1954; Matzinger et al., 1960) were used.

Povilaitis (1967) also showed that the components of the genetic variance varied with the stalk positions. He found that the additive genetic component was higher in the

upper leaves as compared to the bottom leaves for both leaf length and leaf width. On the other hand, the non-additive genetic component (dominance effect) was smaller in the top as compared to the bottom leaves. Based on the same characters, similar observations were also reported by Humphrey et al. (1965).

2.4.6 Heritability

2.4.6.1 Method of estimation

Heritability can be defined as the proportion of observed phenotypic variability which is due to heredity; or more strictly, the proportion of observed variability due to the additive effect of genes (Falconer, 1981). The methods by which the heritability were generally estimated fall into two main categories (Falconer, 1981):

(i) parent-offspring regressions (Falconer, 1981)

(ii) variance components based on the analysis of variance (Gordon et al., 1972; Gordon, 1979).

The use of these methods depends on the design of the experiment and method of analysis. For example, the parent-offspring regression method is normally used when we are dealing with a very small population, and is well utilised by the animal breeders. The procedures and methods of estimation with respect to different relatives were given by Falconer (1981). The analysis of variance method on the other hand is more suitable to the plant breeders since they are normally dealing with a large population under a range of environmental conditions.

By using the variance component analysis, the heritability (h^2) can be defined as follows:

$$h_N^2 = \frac{\sigma_A^2}{\sigma_P^2}$$

$$h_B^2 = \frac{\sigma_G^2}{\sigma_P^2}$$

where σ_A^2 = additive genetic variance, σ_G^2 = total genetic variance, σ_P^2 = total phenotypic variance, h_N^2 = narrow sense heritability estimates and h_B^2 = broad sense heritability estimates. 'Full' or 'restricted' heritability is used based on the components of the denominator. 'Full' heritability is used when all the components of phenotypic variance are used and 'restricted' when any components is removed out of the total phenotypic variance (Gordon et al. 1972; Gordon, 1979). Out of these two, the latter is the one which is normally used and may be termed simply heritability. Even though this simple relationship has been widely used in animal breeding programmes, it has limited use in plant breeding work due to the difficulty in using the reference unit. In plant breeding work, a basic experiment unit is usually a plot which consists of a number of individuals. Based on this concept, Hanson (1963) redefined heritability as 'the fraction of the phenotypic variability for a defined reference unit'. Thus, the more acceptable heritability values for an experiment with 'e' environments, and 'r' replications would be:

$$h_N^2 \text{ (restricted)} = \frac{\sigma_A^2}{\sigma_G^2 + \frac{\sigma_{GE}^2}{r} + \frac{\sigma^2}{re}}$$

This relationship seems to be more acceptable by most plant breeders even though this does not totally solve

the problem since a plot is also a group of individual plants.

2.4.6.2 Heritability and practical plant breeding

Before the concept of heritability can be useful in any breeding programmes, it must be able to relate with the genetic advance and selection concepts. This can be done by using the following basic formula (Falconer, 1981):

$$\begin{aligned}\Delta G &= h^2 i \sigma_p \\ &= \frac{\sigma_A^2}{\sigma_p^2} \cdot i \sigma_p\end{aligned}$$

where ΔG = genetic variance, h^2 = heritability estimate, i = standardised selection differential (selection intensity), σ_p = phenotypic standard deviation, σ_A^2 = additive genetic variance and σ_p^2 = total phenotypic variance. The formula suggested that if the genetic variance of the original population, selection intensity and heritability values are known, then the genetic advance, or expected response can be estimated. It should be realised however the above expressions are utilised in selection among individuals. The expressions for various other selection systems such as among and within family, and combined selections were given by Falconer (1981); and Shelbourne (1969) for tree breeding.

2.4.6.3 Heritability studies in tobacco.

Heritability studies in tobacco have been reported by a number of workers (Povilaitis, 1967; Lamprecht, 1964; Chaudhry and Munshi, 1962; Sastry and Gopinath, 1969).

Povilaitis (1967) showed that the heritability estimates for leaf width ranged from 0.40 (moderately high) for the lower leaves to 0.82 (high) for the upper leaves. The estimate for leaf length ranged from 0.27 (low) for lower leaves to 0.57 (moderately high) for the upper leaves. The higher estimates in the upper leaves indicate that environment has less influence on the phenotypic variability as compared to the lower leaves. This is compatible with the variance components analysis reported by Humphrey et al. (1965) and Povilaitis (1967). They showed that the additive genetic variance, which was the main component of genetic variance for these traits were higher in the upper as compared to the lower leaves (See Section 2.4.5). When the data were averaged across all the leaf positions, the heritability estimates for leaf width and length were found to be 0.59 and 0.38 respectively. This seems to agree with the results obtained by Lamprecht (1964). By using the mean of all harvestible leaves, he found that the heritability estimates were 0.46 for leaf width and 0.56 for leaf length. Chaudhry and Munshi (1962) reported that the heritability estimates of 0.39 and 0.43 were obtained for leaf width and length respectively.

Heritability estimate for leaf shape (length/width) was reported to be 0.75 (Chaudhry and Munshi, 1962). This is much higher than leaf width and length estimates reported by them. This indicates that leaf shape (length/width) is less affected by the environment as compared to leaf width and leaf length. Higher estimates were obtained by Gordon (1967). He showed that the

estimates for top, middle and bottom leaves were 0.91, 0.95, and 0.80 respectively.

2.4.7 Heterosis: Possible use of F_1 hybrids in tobacco breeding programmes

Heterosis can be defined as the percentage increase of F_1 hybrids over the mid-parent (Poehlman, 1979). However, some workers use the better parent as the basis of comparison and is often referred as heterobeliosis (Virk and Verma, 1973). The latter definition is more appropriate if we are concerned with producing a commercial hybrid variety.

The presence of heterosis has been reported for a number of plants and some of these have been used commercially. A list of some commercially used hybrid varieties in food crops is given by Sinha and Khanna (1975).

Evidence of heterosis for various characters has also been reported in tobacco (Matzinger and Mann, 1962; Matzinger et al., 1962, 1971; Mann et al., 1962; Aycock et al., 1963; Marani and Sachs, 1966; Povilaitis, 1966, 1971, 1972; Matzinger and Wernsman, 1967, 1968; Vanderberg and Matzinger, 1970; Dubey, 1976a,b; Dubey and Rao, 1976; Aycock, 1977; Jones and Henderson, 1978; Keyes et al., 1981). These studies were made either for crosses within or between each type of tobacco that is Virginian flue-cured, Burley or Oriental types. With respect to that, even though tobacco is a self pollinating crop it may still be worth the effort to locate the F_1 hybrids for commercial production. This is mainly due to the fact that crossing can be easily done and seed yield is

very high. Hence hybrid seed should be cheap.

In the past, F_1 hybrids have been used in tobacco breeding programmes to incorporate certain characters that are difficult to obtain in homozygous condition in useful cultivar. Such example includes the production of disease resistance hybrid variety such as GA 1470. This particular cultivar which is resistant to black shank and bacterial wilt was developed from male sterile Hicks (Anonymous, 1971; Byrd, 1972). The decision whether the F_1 hybrid or homozygous pure line should be maintained however depends on the type of predominant gene action observed, the extent of heterosis and the urgency of having such specific character in question. With respect to that F_1 hybrids in tobacco are usually used as a temporary measure until a suitable homozygous lines are available.

Heterosis studies on leaf size characters such as leaf length and leaf width have been reported by a number of workers (Matzinger et al., 1962; Jabar, 1967; Vanderberg and Matzinger, 1970; Dubey, 1976a,b; Dubey and Rao, 1976). In majority of these crosses, the F_1 values were significantly bigger than the mid parent value. However, there are some cross combinations where the F_1 values were much bigger than the broad or longer-leaved parents (Dubey, 1976; Dubey and Rao, 1976). They found that the laminar area and leaf width of the F_1 hybrids were larger than the better parents by up to 76 % and 125 % respectively.

2.4.8 Correlation Studies

Genotypic and phenotypic correlation coefficients can be estimated and may be useful in planning breeding

programmes. This is especially so when the economic evaluation of the crop depends upon a small number of traits. To the plant breeder, this will help to formulate the most effective method of breeding and to simplify the approach to selection. For example selections based on only one important trait may be carried out if it is highly correlated with other desirable traits.

Correlation coefficient (r) between trait X and trait Y can be defined as the ratio of covariance between X and Y to the product of their standard deviations (Draper and Smith, 1981; Steel and Torrie, 1980). This can be represented as follows:

$$r = \frac{(X-\bar{X})(Y-\bar{Y})/(n-1)}{\sqrt{\sum(X-\bar{X})^2/(n-1)} \cdot \sqrt{\sum(Y-\bar{Y})^2/(n-1)}}$$

where $(X-\bar{X})(Y-\bar{Y})/(n-1)$ = the covariance between trait X and trait Y , $\sqrt{\sum(X-\bar{X})^2/(n-1)}$ = standard deviation of trait X and $\sqrt{\sum(Y-\bar{Y})^2/(n-1)}$ = standard deviation of trait Y .

Such techniques have been widely reported in tobacco breeding programmes. Correlation coefficients between some traits as reported by some workers are shown in Table 2.1. By studying the phenotypic and various genetic variances correlation coefficients between a number of traits, Povilaitis (1965) generally showed that the additive genetic correlation coefficients were larger than the phenotypic correlation coefficients. He also showed that the high phenotypic correlation coefficients were associated with high additive genetic and genotypic correlation coefficients. On the other hand, low phenotypic correlation coefficients were associated with

TABLE 2.1
 PHENOTYPIC (r_P), GENOTYPIC (r_G), AND ADDITIVE GENETIC (r_A)
 CORRELATION COEFFICIENTS BETWEEN PAIRS OF
 CHARACTERS AS REPORTED BY SOME WORKERS.

CHARACTERS	Correlation coefficients			Reported by:
	r_P	r_G	r_A	
length and - width	0.91** 0.27*		0.59**	Rosa, 1979 Legg and Collins, 1971a
	0.45*** 0.62***	0.52	0.69	Povilaitis, 1967 Povilaitis, 1965
- midrib	0.77**			Sastry and Gopinath 1969
- yield	0.90**			Ogilvie, 1979
- days to flower	0.61***	1.01	0.91	Povilaitis, 1965
- number of leaves	0.69***	0.98	1.70	Povilaitis, 1965
- plant height	0.76***	0.98	1.12	Povilaitis, 1965
- lamina weight	0.36*			Rosa, 1979
width and - midrib	0.44**			Sastry and Gopinath 1969
- days to flower	0.36***	0.62	0.97	Povilaitis, 1965
- number of leaves	0.34***	0.44	1.35	Povilaitis, 1965
- plant height	0.57***	0.63	1.41	Povilaitis, 1965
- yield	0.35*		0.58*	Legg and Collins, 1971a
	0.65**			Ogilvie, 1979
- lamina weight	0.51*			Rosa, 1979
stalk position and - trichome number	0.93**			Tso, <u>et al.</u> , 1977
- leaf thickness	0.64**			Tso, <u>et al.</u> , 1977

N.B.:

- (i) * - significant at $p = 0.05$
 ** - significant at $p = 0.01$
 *** - significant at $p = 0.001$

- (ii) Levels of significance were not given where there were no tests of significance reported.

low additive genetic and genotypic correlation coefficients. This probably indicated that the influence of environment was high for these pairs of characters. The phenotypic and genotypic correlation coefficients were high between leaf length and days to flowering, number of leaves and plant height. In contrast to that, for the same correlation coefficients, the values were found to be smaller for the leaf width and the above characters (See Table 2.1).

Phenotypic correlation coefficients between length and width were also reported by several workers (Table 2.1). Povilaitis (1964) also showed that there was a significant negative between leaf width and length for the top leaf. This correlation however become positive and increased progressively for each lower position of the leaf.

Correlation coefficients between some other characters are also presented in Table 2.1.

3. MATERIALS AND METHODS

3.1 PARENTAL LINES

The study was initiated by sampling twenty-nine (29) genotypes from a tobacco germplasm collection. These genotypes were mostly dihaploids derived from the pollen culture experiments, and represented a random sample of the various types of leaf shape characters available in New Zealand. The leaf shape characters of these genotypes were studied by growing them in glasshouse conditions.

By using stratified random sampling, eight (8) genotypes were drawn from the germplasm. This strata were defined with respect to leaf shape (length/width), length of the petiole and auricle size variation found in the collection. These genotypes also varied in other characters such as angle of venation, leaf tip shape, leaf area, and width of the wing. These sampled genotypes were used for the diallel mating.

A detailed description of the strata is shown in Table 3.1 and Plate 3.1. More than one parental lines were sampled for some of the strata. This is because some strata were not found in the collection.

3.2 MATING DESIGN

A half diallel was used (i.e. no reciprocals and only one set of crosses - method 2 of Griffing (1956)). This design was chosen since it has been shown that there is no reciprocal effect for leaf characters in tobacco studied to date (Jinks, 1954; Van der Veen, 1957; Van

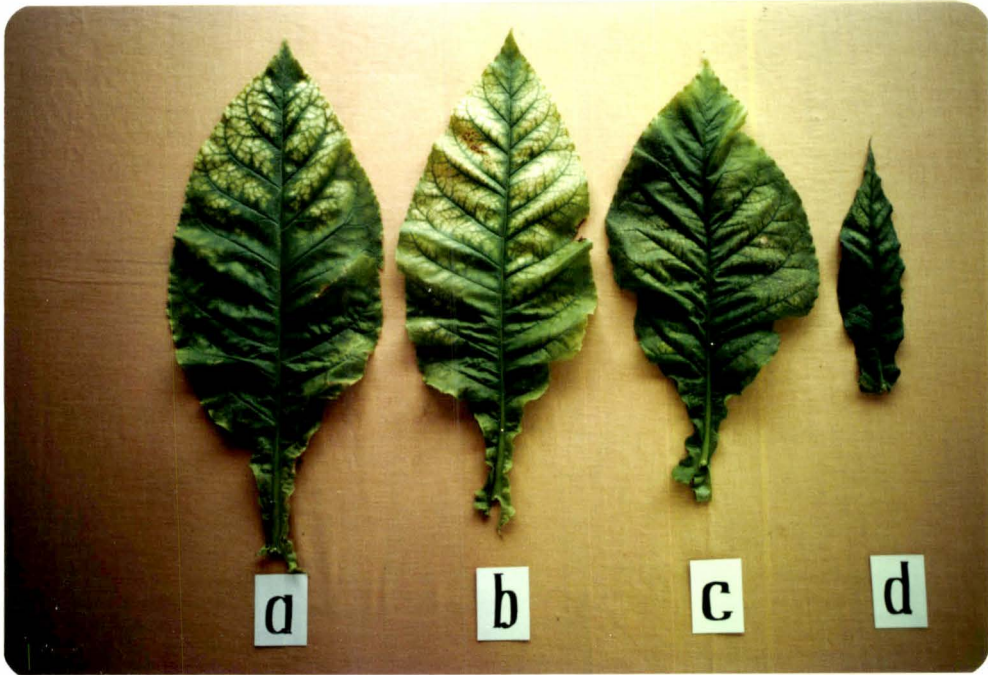
TABLE 3.1
THE PARENTAL NUMBERS, GENOTYPES, AND THE STRATA USED TO SAMPLE
THE PARENTAL LINES

PARENTAL NUMBER	GENOTYPE	STRATA USED TO SAMPLE THE PARENTAL LINES		
		LEAF SHAPE LENGTH/WIDTH	PETIOLE LENGTH	AURICLE WIDTH
1	TI 1371	wide leaf	long	narrow
2	HFCA 207	wide leaf	short	wide
3	HFCA 220	wide leaf	short	wide
4	20728-92	narrow leaf	long	narrow
5	HFCA 250	narrow leaf	long	narrow
6	HFCA 168	narrow leaf	long	narrow
7	KUAKA 860	medium leaf	long	narrow
8	HFCA 241	medium leaf	long	wide

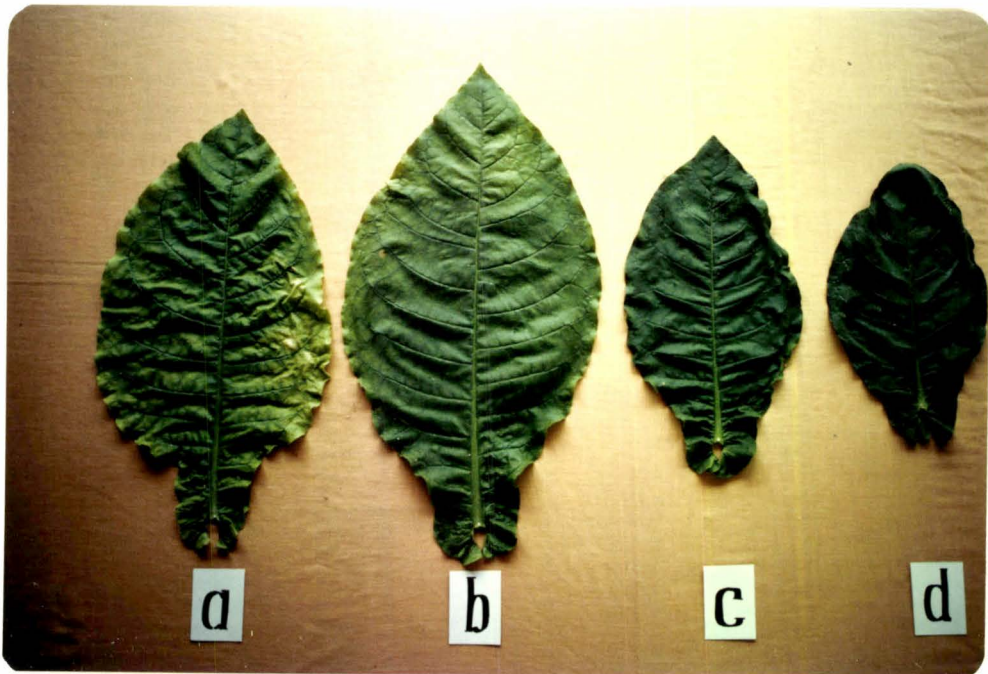
PLATE 3.1

LEAF CHARACTERISTICS OF THE PARENTS
USED IN THE CROSSES

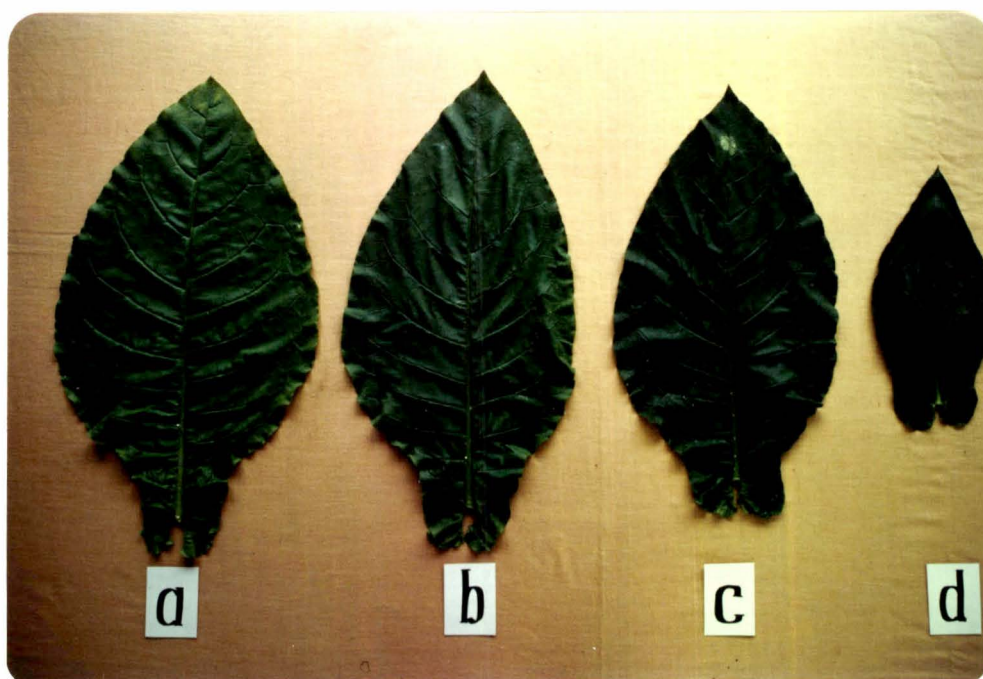
- (a) 17th LEAF
- (b) 12th LEAF
- (c) 7th LEAF
- (d) 2nd LEAF



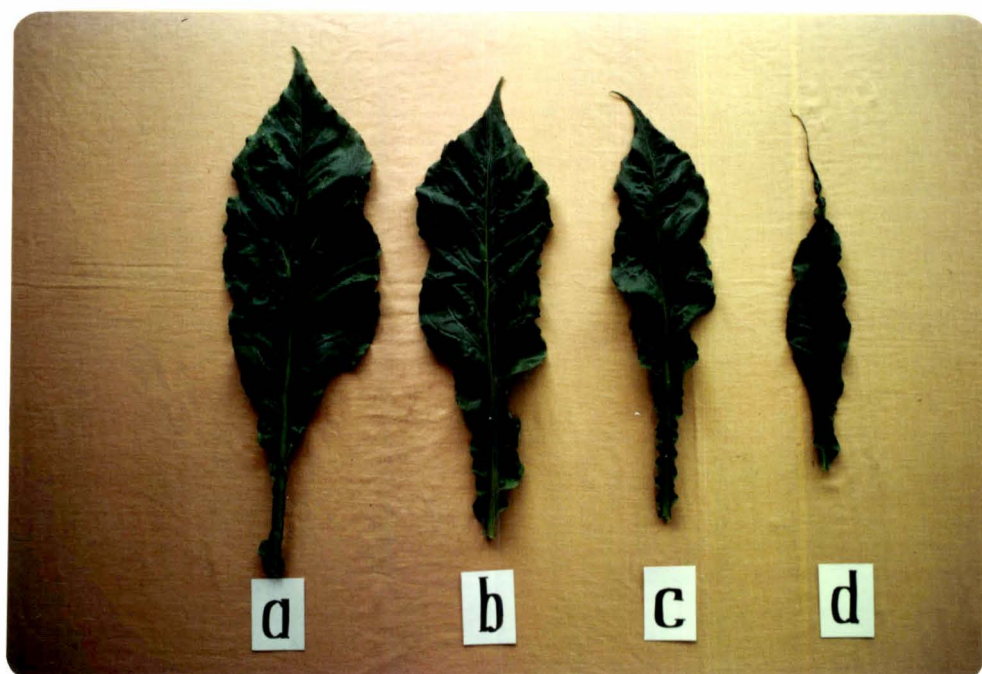
PARENT 1 (TI 1372)



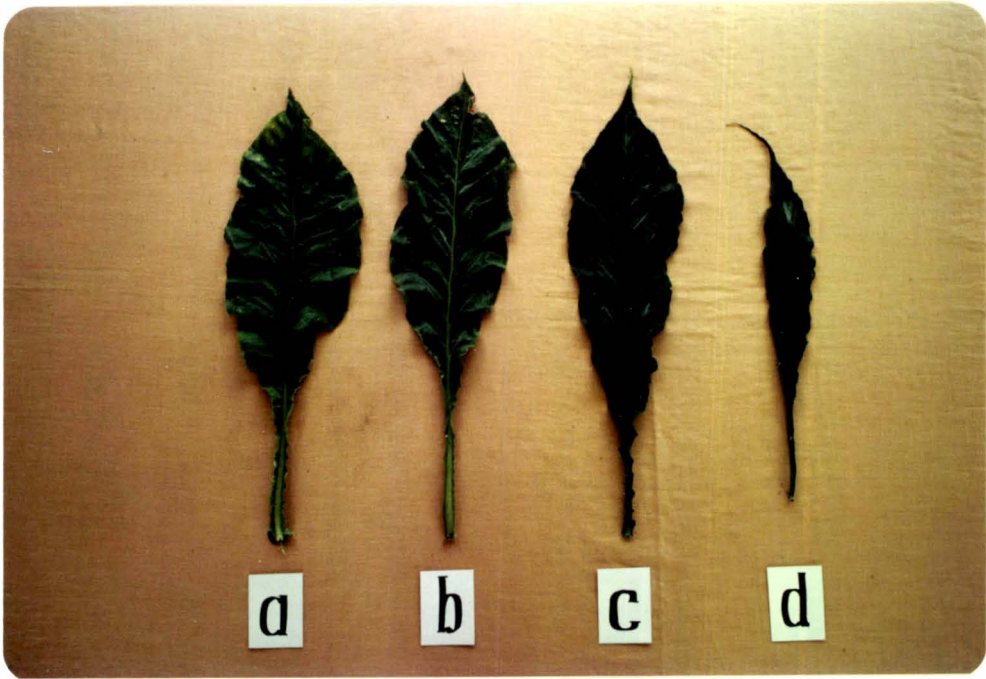
PARENT 2 (HFCA 207)



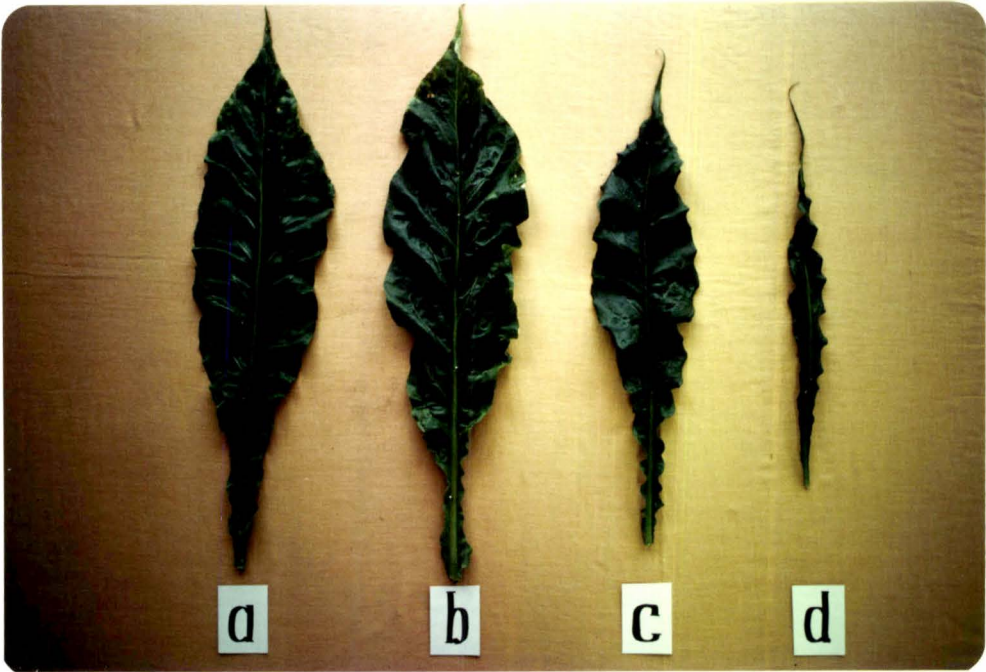
PARENT 3 (HFCA 220)



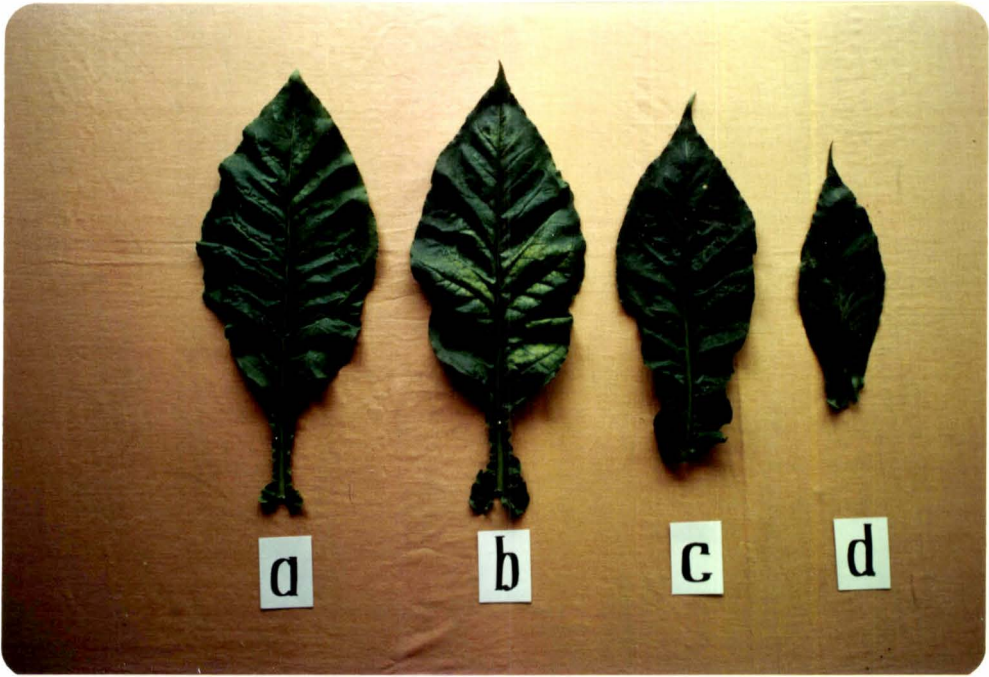
PARENT 4 (20728-92)



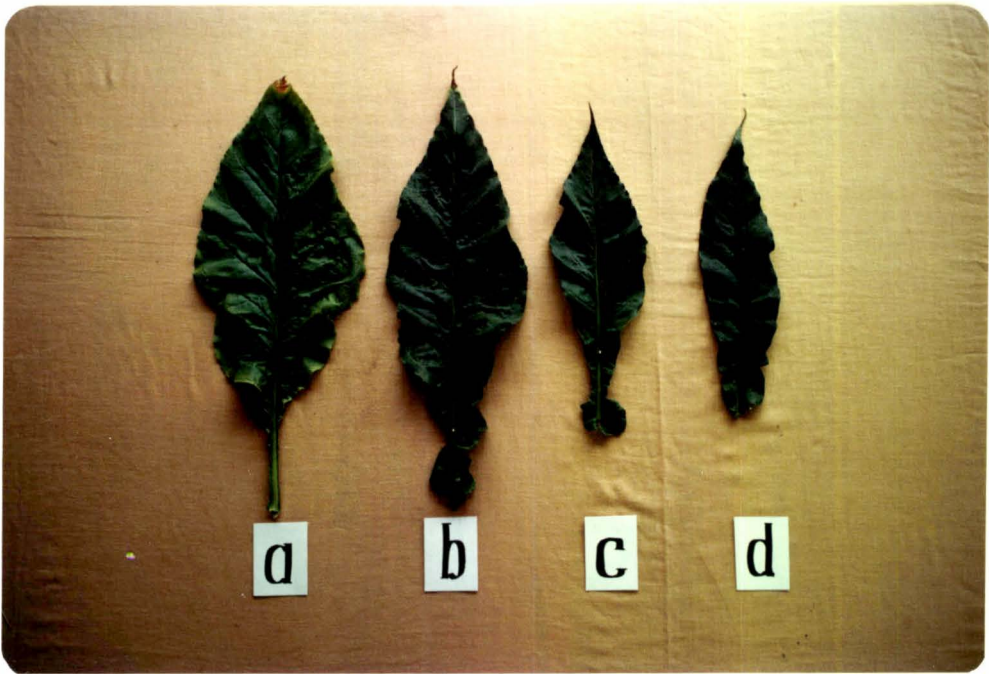
PARENT 5 (HFCA 250)



PARENT 6 (HFCA 168)



PARENT 7 (KUAKA 860)



PARENT 8 (HFCA 241)

der Veen and Bink, 1961; Matzinger et al., 1962; Ogilvie and Kozumplik, 1980). In addition to that there was insufficient space in the glasshouse for a full diallel with a reasonable number of parental lines (i.e. 8 parental lines).

With 8 parents in all possible cross combinations, a total of 36 genotypes (28 hybrids and 8 parents) were produced. By using the parental number of Table 2.1, these 36 genotypes were coded as in the following examples: (11) is the selfed parent 1 (i.e. TI 1372) and (21) is the hybrid between parent 2 (i.e. HFCA 207) (female) and parent 1 (i.e. TI 1372) (male). These codes will be referred as genotypes in later discussions.

3.3 EXPERIMENTAL DESIGN AND MANAGEMENT OF PLANT MATERIALS

The experiment was carried out under glasshouse conditions. A completely randomised block design was used with 3 replications. Each plot consisted of two plants in individual planter-bags.

Small pots were initially used to establish the seedlings. One pot was provided for each plot in the main experiment. These nursery pots were randomised as in the main plots. This ensured that the possible influence of the nursery pots during the establishment period had no effect in the later main plot carryover. Mather and Jinks found this to be a problem with N. rustica (Mather and Jinks, 1977) and they recommended taking these precautions.

The seeds germinated after 1 week from sowing.

Frequent thinnings were carried out to get an even seedling growth in the seedling pots. At 5 weeks after germination (3-4 leaf stage), after hardening, the seedlings were selected for uniformity and transplanted into size 18 (20 cm x 20 cm x 20 cm) plastic planter-bags. Each bag received 2 plants, which were thinned to 1 a week later.

A standard potting mixture (sand : peat :: 5 : 2) was used. Nutrients were supplied by Osmocote[®] (N : P : K :: 14.0 : 16.1 : 11.6), a slow-releasing fertiliser (3-4 months duration). Fifty millilitres of Osmocote was mixed with every 10 litres of the potting mixture.

The plants were hand watered daily. White flies and aphids were controlled with Vapona[®] (a.i. = dichlorvos at 1080 g/l). Benlate[®] (a.i. = benomyl at 50 % W/W) was used to control powdery mildew.

The glasshouse temperature was maintained at about $23 \pm 2^{\circ}$ C. However natural diurnal fluctuations from $16 \pm 2^{\circ}$ C at night to $26 \pm 2^{\circ}$ C during a hot day did occur despite the temperature maintenance equipment.

3.4 CHARACTERS MEASURED

3.4.1 Leaf definition and management

To facilitate the study of leaf characters, the removal of the flower head (topping) was not carried out. This will reduce the frequency of desuckering or removal of lateral buds required. It has been shown that topping has little effect on leaf shape (Gordon, 1969). However small cotyledonous leaves were removed.

The 2nd, 7th, 12th, and 17th leaf from the top were harvested to represent the 'tip', 'leaf', 'cutter' and 'lug' respectively. The uppermost leaf was defined as the first below the lowest inflorescence branch. The inflorescence branch had no leaf upon it and thus it can be easily differentiated from the uppermost sucker (lateral branch). These leaves were harvested as they matured. Mature leaf was defined as having yellowish green colour with patches of green along the midrib and lateral veins. This was not necessarily the same ripeness as would be used for commercial harvest.

3.4.2 Measurement of leaf-shape and other characters

These measurements were preceded by tracing accurately the outline of the leaf on to plain paper. Except for vein angle and leaf dry weight, all measurements were made on these outlines. The characters measured and used for further analyses were:

(1) leaf ratio (length (L) / width (W)) - (Figure 3.1)

where L = leaf length measured from the base of
of the petiole to the tip of the leaf
(cm)

W = leaf width measured at the widest point
along the midrib (cm).

This ratio has been used often to describe the leaf shape in tobacco (Van der Veen, 1957; Van der Veen and Bink, 1961; Chaudhry and Munshi, 1962; Povilaitis, 1965; Sastry and Gopinath, 1969; Gordon, 1969; Eugechi, 1971). It includes aspects of tip, lamina and wing shapes and petiole length.

(2) Differential index - (Figure 3.2). This gives a

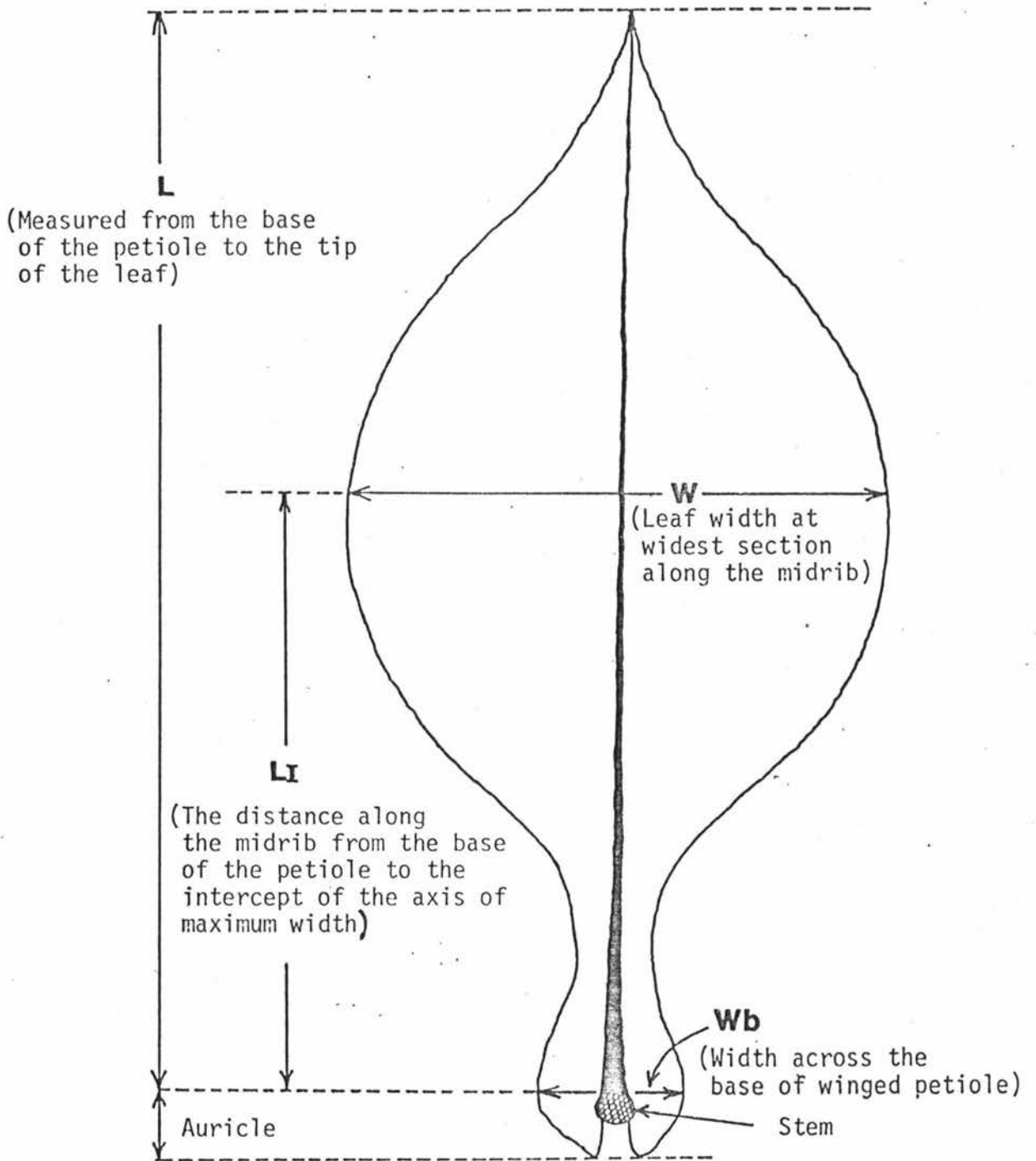


FIGURE 3.1 ILLUSTRATION OF LEAF CHARACTERS MEASURED TO OBTAIN LEAF RATIO AND RAPER'S INDICES

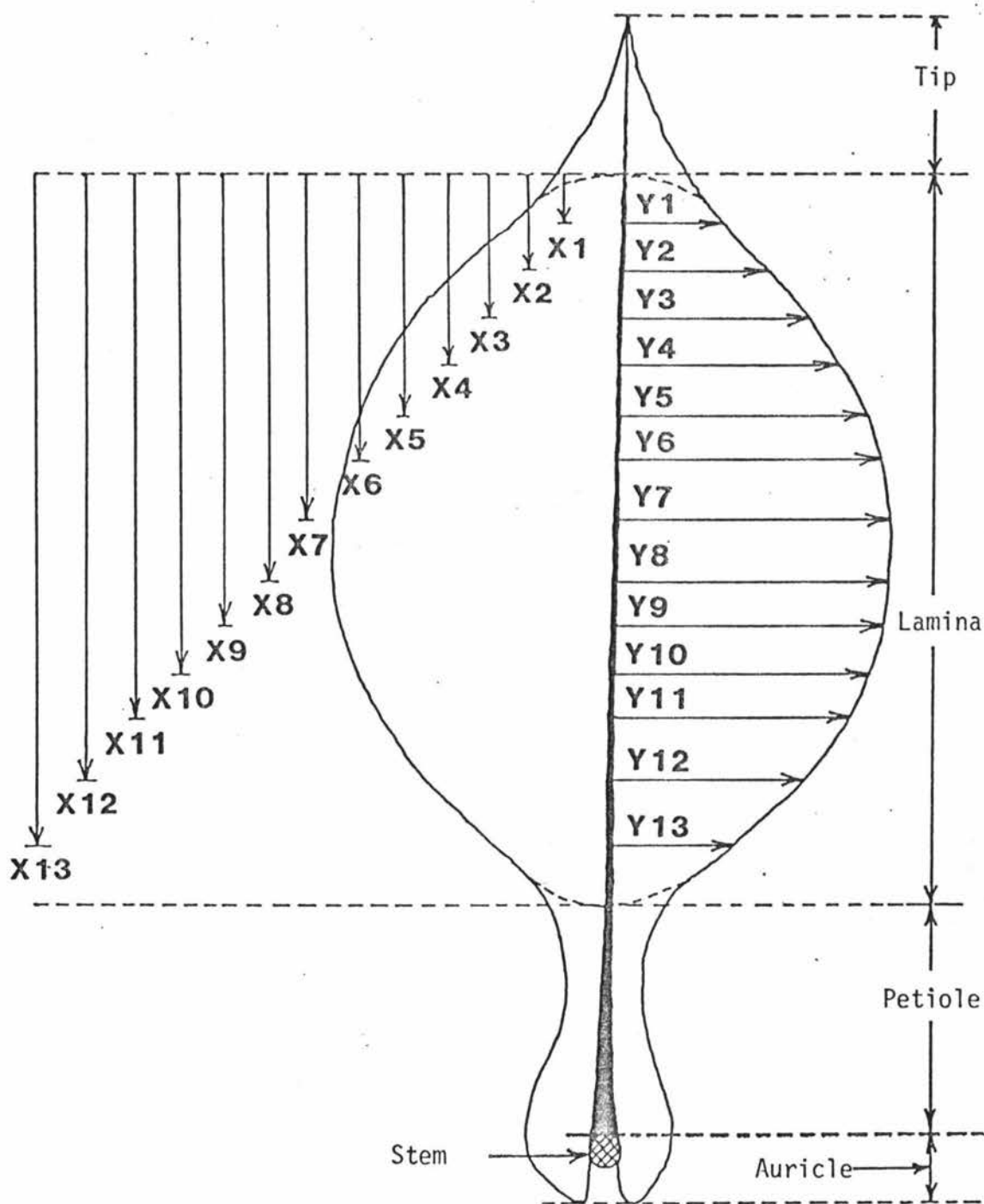


FIGURE 3.2 ILLUSTRATION OF MEASUREMENTS TAKEN TO OBTAIN DIFFERENTIAL INDEX AND ASSOCIATED TIP AND PETIOLE LENGTHS

direct measure of the shape of the main lamina region. It therefore is a more appropriate measure of leaf shape, as the lamina constitute the main portion of the leaf. By regressing half leaf width to length along midrib from the tip, the following quadratic relationship was obtained:

$$y = \hat{b}_0 + \hat{b}_1x + \hat{b}_2x^2$$

where y = distance from midrib to margin (mm),
 x = distance along midrib from the datum (mm),
 and $\hat{b}_0$, $\hat{b}_1$ and $\hat{b}_2$ are the regression coefficients. This functional relationship was statistically acceptable since the coefficient of determination (R^2) of the regression equations obtained were generally high (approximately 0.7). The x and y measurements were made only on the main laminar area (i.e. excluding the tip and leaf base). In going along the margin from the region of maximum width towards the petiole, a more or less inward curve (sinus) was observed. Based on the position of this sinus and the curvature of the margin at this point, a subjective line was drawn from the margin to the midrib. This line was used to define the 'cut-off' between the wing and the laminar area. The point in which this line cuts the midrib was defined as the lamina base (See Figure 3.2). A similar procedure was carried out to define the 'cut-off' between the tip and actual lamina area. Depending on the length of the leaf, the intervals used along

the midrib ranged from 2 - 4 cm. About 12 pairs of x and y measurements were taken per leaf. By differentiating the functional relationship $y = \hat{b}_0 + \hat{b}_1x + \hat{b}_2x^2$ with respect to x,

$$\frac{dy}{dx} = \hat{b}_1 + 2\hat{b}_2x^2 \quad (= \text{rate of change of margin position with respect to midrib position})$$

$$\text{and } \frac{d^2y}{dx^2} = 2\hat{b}_2 \quad (= \text{rate of change of the change of margin position}).$$

This value ($2\hat{b}_2$), after multiplying by 100, was used as a single index of leaf shape. Due to the amount of work involved and time limitation, this functional relationship was obtained for one half the leaf only. It was assumed that it would have only a trivial effect on the estimate of leaf-shape. SPSS/REGRESSION (Nie et al., 1975) was used to estimate the regression equations.

- (3) Raper's index I (L/L_I) - Raper et al. (1974)
(Figure 3.1),

where L_I = the distance along the midrib from the base of the petiole to the intercept of the axis of maximum width (cm),

and L as in (1). This ratio indicates the relative position of the widest section of the leaf along the midrib.

- (4) Raper's index II (W/W_b) - Raper et al. (1974)
(Figure 3.1)

where W_b = the width across the base of the winged petiole (cm)
and W as in (1).

(5) Tip score.

The score given ranged from 1 to 5 with 1 the most rounded and 5 the most attenuated as shown in Figure 3.3. These scores were first normalised before other analyses were performed.

(6) Petiole length (mm) - Figure 3.4

The length from the 'lamina base' to the origin at the stalk. 'Lamina base' was defined as in (2).

(7) Wing width (mm). - Figure 3.4

This was measured at the narrowest point along the midrib.

(8) Wing area (cm^2) - Figure 3.4

A line was drawn across the leaf base at the end of the petiole to define the 'cut-off' between the wing and auricle area. The 'cut-off' between the lamina and wing area was defined as in (2). From the outline of the leaf on the paper, the area which was represented by the wing was cut out. A leaf area meter was then used to estimate the area of the paper cut-out.

(9) Auricle area (cm^2) - Figure 3.4

As in (8), using the paper cut-outs of the auricles.

(10) Vein angle (degrees) - Figure 3.4

Vein angle measurements were taken at three positions on both halves of the fresh leaf: at laminar base, at the point of widest leaf

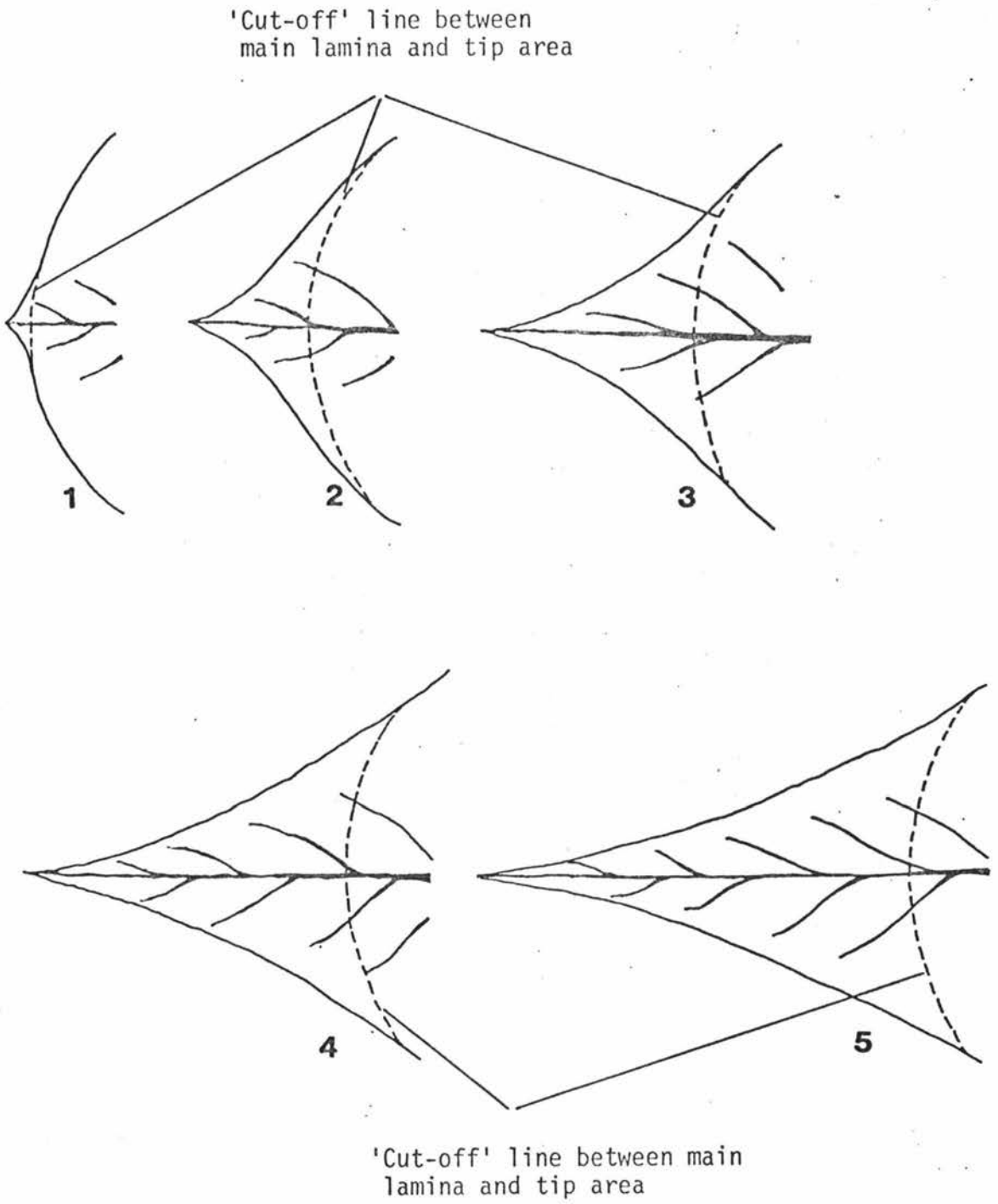


FIGURE 3.3 LEAF TIP SCORES

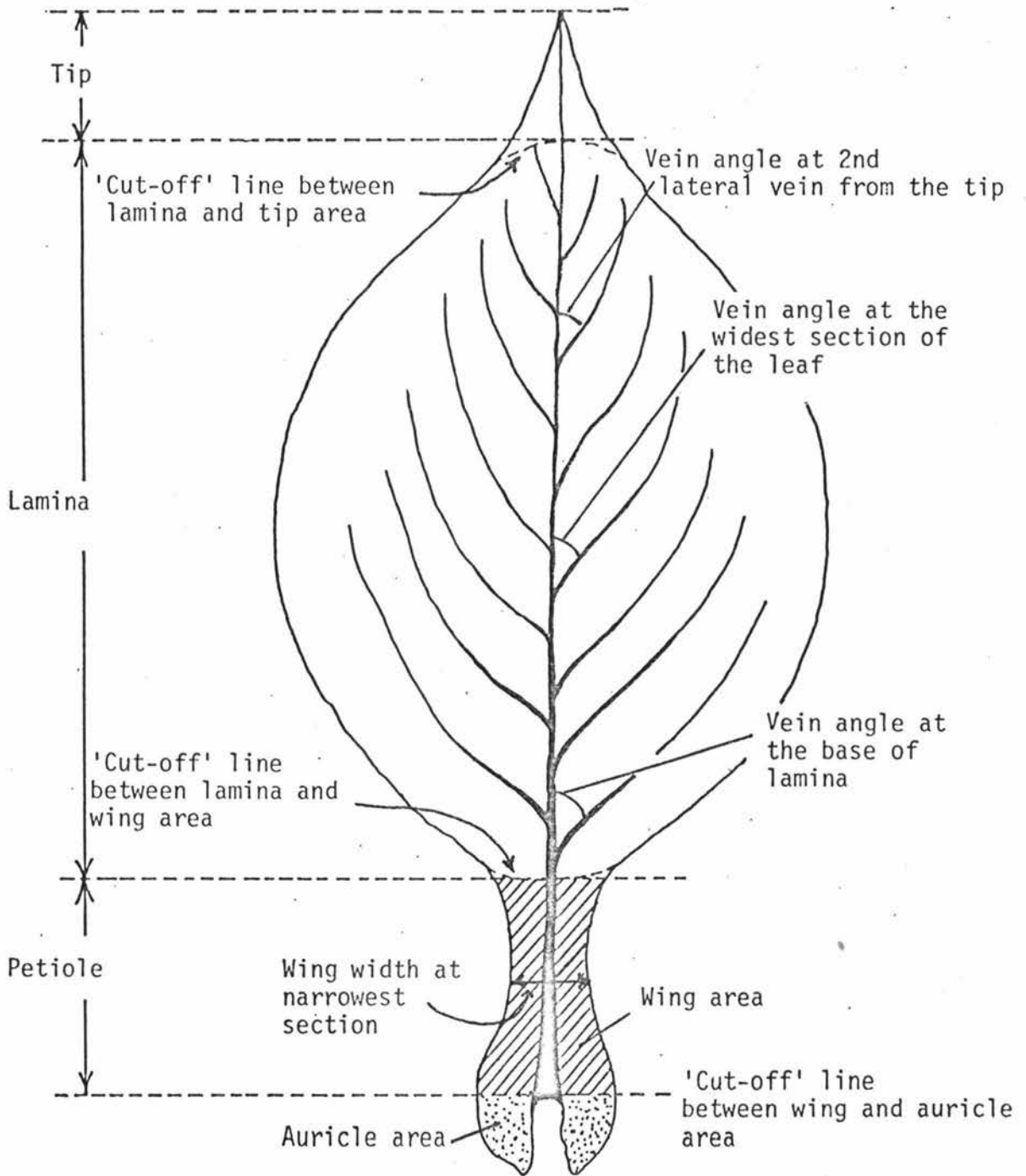


FIGURE 3.4 ILLUSTRATION OF OTHER CHARACTERS MEASURED

width and at the 2nd lateral vein from the tip. The measurements were taken on the upper surface of the leaf, facing towards the tip. The mean value obtained from these measurements was used as a single measurement of vein angle in the subsequent analyses.

(11) Leaf dry weight (g)

The weight was taken after oven drying at 60°C for 24 hours (Lamprecht and Botha, 1975).

(12) Leaf area (cm^2) - Figure 3.4

The method used to determine the leaf area was similar to that of McKee and Yocum (1970). The traced outline on the paper which included tip, main lamina, wing and auricle area was carefully cut out and weighed to the nearest milligram. A factor ($164.3475 \text{ cm}^2/\text{g}$) was then used to convert the paper weight to leaf area. This conversion factor was calculated based on 30 random samples of the known area (300 cm^2) of the same paper. The mean ($\bar{X}$) and standard deviation (σ) of the weight (g) of the paper used were 1.8254 and 0.0148 respectively.

For each character measured, value obtained from the mean of the two plants was used as the plot value for subsequent analysis.

3.5 ANALYSIS OF THE DATA

In the analysis it was assumed that the parental lines constituted a stratified random sample from a

self pollinated base population representing germplasm of interest in New Zealand. They were considered to represent well the range of leaf shape characters available in flue-cured tobacco. The statistics obtained from this analysis estimated the parameters of this base population (i.e. a random effect model - Model II of Eisenhart (1947) - was used).

3.5.1 Analysis of variance

The analysis of variance as described by Steel and Torrie (1980) was carried out by using a computer programme PHANIE (Phenotypic Analysis in Environments) (Gordon, unpublished).

The analysis was based on the random effect model for randomised complete block design in single environment. The model is:

$$X_{ij} = \mu + \gamma_i + \beta_j + \epsilon_{ij}$$

where X_{ij} = X_{ij} th phenotypic observation, μ = population mean, γ_i = i th genotype population effect, β_j = j th block effect, ϵ_{ij} = residual variation associated with ij th observation, $i = 1 \dots g$ genotypes and $j = 1 \dots b$ blocks. All effects were assumed random, independent deviates with expectation equal to zero and generating variances of corresponding designation.

The expectation of mean squares, together with appropriate F tests, are given in Table 3.2.

Diallel analysis and heritability estimates were carried out only for the characters where these analyses of variance showed the presence of genotypic variability.

TABLE 3.2
 EXPECTATION OF MEAN SQUARES FOR RANDOM
 EFFECT IN SINGLE ENVIRONMENT

$$\text{MODEL: } X_{ij} = \mu + \gamma_i + \beta_j + \epsilon_{ij}$$

Source	df	MS	E (MS)	F
Blocks	(b-1)	MS_1	$\sigma^2 + g\sigma^2_B$	MS_1/MS_3
Genotypes	(g-1)	MS_2	$\sigma^2 + b\sigma^2_G$	MS_2/MS_3
Error	(b-1)(g-1)	MS_3	σ^2	
Total	(bg-1)			

3.5.2 Diallel analysis

The notations used, and the analysis of the diallel tables were carried out according to the method of Mather and Jinks (1971). In their approach, the V_r (variance for each array) and W_r (covariance between the parents and their offsprings) were estimated and these were then used to test the adequacy of the additive-dominance model. The mean of V_r and W_r across the three blocks were used to estimate the second degree statistics and consequently the estimate of genetical variances. Information on the characteristics of the dominance were also obtained.

3.5.2.1 Tests of the adequacy of the additive-dominance model

The adequacy of the additive-dominance model (Hayman, 1954) was tested by:

- (i) the homogeneity of $(W_r - V_r)$.

Homogeneous $(W_r - V_r)$ indicated that inter-locus interaction (epistasis) was absent. The presence of dominance was indicated by the heterogeneous $(W_r + V_r)$. Analyses of variance were used to test the homogeneity of both $(W_r - V_r)$ and $(W_r + V_r)$. Both the analyses of variance of $(W_r - V_r)$ and $(W_r + V_r)$ were carried out by using a computer programme GENSTAT (GENERAL STATISTICS) (Alvey *et al.*, 1977).

- (ii) Significant deviation of (W_r, V_r) regression coefficient ($\hat{b}_1$) from unity. The test of the significant deviation of $\hat{b}_1$ from unity was carried out by using t - test (Draper and Smith,

1981; Steel and Torrie, 1980). To test the hypothesis that $\hat{b}_1 = 1$, t was computed as,

$$t = \frac{\hat{b}_1 - 1}{\text{s.e.}(\hat{b}_1)}$$

where $\hat{b}_1$ = regression coefficient, and $\text{s.e.}(\hat{b}_1)$ = standard error of $\hat{b}_1$ ($= \sqrt{\sigma^2 / (\sum (X_i - \bar{X})^2)}$). The calculated t value was then compared to the tabulated $|t|$ with $(n-2)$ degree of freedom where n = number of observations. A computer programme SPSS/REGRESSION (Nie et al., 1975) was used to estimate the regression coefficient.

In cases where the data sets did not conform to the additive-dominance model, all parents were deleted individually (i.e. parent 1 to 8), in turn. These new sets of 7 x 7 diallel data were then reanalysed and tested. Further analyses on these new sets of data were performed only when they satisfied the model.

In cases where none of these 7 x 7 reanalysed did agree with the model, all genetical interpretations were based only on the 8 x 8 original data. It has been pointed out by Mather and Jinks (1971) and Hayman (1954) that it is still possible to make estimates of the population parameters and genetic components from such sets of data.

3.5.2.2 Second degree statistics

By using a single gene difference A-a as an example, the diallel table obtained by mating two inbred lines is shown in Table 3.3. The effects of three possible

genotypes AA, Aa and aa were represented as $\underline{d_a}$, $\underline{h_a}$, and $-\underline{d_a}$, respectively. The frequencies of A and a were $\underline{U_a}$ and $\underline{V_a}$ respectively (See Section 2.4.4).

Based on this the following second degree statistics were estimated:

$$\bar{Vr} = U_a V_a (d_a - (U_a - V_a) h_a)^2 - (\text{mean variance of the arrays})$$

$$\bar{Wr} = 2U_a V_a d_a^2 - 2U_a V_a (U_a - V_a) d_a h_a - (\text{mean covariance between the parent and their offsprings of the arrays})$$

$$V\bar{r} = \frac{1}{2} ((U_a d_a + V_a h_a) + (U_a h_a - V_a d_a)) - (U_a d_a + V_a h_a + U_a h_a - V_a d_a)^2 - (\text{variance of the array means})$$

$$Vp = 4 U_a V_a d_a^2 - (\text{variance of the parents}).$$

3.5.2.3 Estimates of genetical components

From the second degree statistics obtained in Section 3.5.2.2, the genetical components were estimated by using the following estimators. (The derivation of these relationships, from those of the full diallel model given by Mather and Jinks (1971), is presented in Appendix 1).

$$\hat{D} = Vp - E$$

$$\hat{H}_1 = 4Vr - 4Wr + V_p - \frac{5n - 4}{n} E$$

$$\hat{H}_2 = 4Vr - 4Wr - \frac{4(n - 1)}{n} E$$

$$\hat{F} = 2Vp - 4Wr - \frac{2(n - 2)}{n} E$$

The error term E used was the pooled error variance obtained from the analysis of variance (Section 3.5.1).

TABLE 3.3

DIALLEL TABLE FOR THE FOUR FAMILIES OBTAINED
BY MATING TWO TRUE-BREEDING LINES
DIFFERING IN ONE GENE, A-a
(SEE TEXT FOR DEFINITIONS)

Female Parent			
Male	AA	aa	Row
Parent	U_a d_a	V_a $-d_a$	Mean
AA	AA	Aa	
U_a	U_a^2	$U_a V_a$	$U_a d_a + V_a h_a$
d_a	d_a	h_a	
aa	Aa	aa	
V_a	$U_a V_a$	V_a^2	$-V_a d_a + U_a h_a$
$-d_a$	h_a	$-d_a$	
Column mean	$U_a d_a + V_a h_a$	$-V_a d_a + U_a h_a$	Overall mean $(U_a - V_a) d_a + 2U_a V_a h_a$

The assumption was made that this measure of environmental variance would be appropriate for both the parents and the hybrids. It was observed that the pooled error variance obtained were generally similar to that of the hybrids or the parents.

These components of variations were then used to compute the following ratios:

$$\sqrt{\hat{H}_1 / \hat{D}} = \text{mean degree of dominance over all loci (0 to 1 indicating partial dominance; 1 - complete and 1 - over dominance) (Hayman, 1954; Mather and Jinks, 1971).}$$

$$\hat{H} / (4 \hat{H}_2) = (\overline{UV}) = \text{an estimate of average frequency of positive (U) and negative (V) alleles in the parents, where } U + V = 1.$$

$$\frac{1}{2} F / \sqrt{\hat{D} (\hat{H}_1 - \hat{H}_2)} = \text{consistency of distribution of dominance and recessive alleles across the loci (} \pm 1 - \text{ constant) (Mather and Jinks, 1971).}$$

$$\frac{\sqrt{4 \hat{D} \hat{H}_1} + \hat{F}}{\sqrt{4 \hat{D} \hat{H}_1} - \hat{F}} = \frac{K_D}{K_R} = \text{ratio of total number of dominant to recessive genes in all the parents (Hayman, 1954).}$$

3.4.2.4 Graphical analysis

The relative distribution of the dominant and recessive genes in the parental lines were shown by the relative positions of (Wr, Vr) points on the (Wr, Vr) regression lines and the associated parabolas plotted (Hayman, 1954). Parents having most dominant genes

occupy the lower position of the regression line nearer to the origin. Those which occupy the upper position of the regression line have more recessive genes. Completely dominant and recessive parents will coincide with the lower and upper points of intersections between the regression line and the parabola (Hayman, 1954).

In obtaining the (W_r , V_r) regression equations, all individual values of W_r and V_r were used. However only the mean of W_r and V_r across the 3 blocks were used to represent the position of the parental lines on the graphs.

Regression lines were obtained by using a computer programme SPSS/REGRESSION (Nie et al., 1975).

3.5.2.5 Direction of dominance

The direction of dominance was obtained from the correlation coefficients (r) between ($W_r + V_r$) and $\bar{P}$ (parental mean). Negative and significant coefficients indicated that the parents having higher phenotypic mean were dominant to those having lower phenotypic mean. Positive and significant coefficients indicated that the parents having lower phenotypic mean were dominant.

All values of ($W_r + V_r$) and $\bar{P}$ for the three blocks were used in estimating the correlation coefficients.

Correlation coefficients were estimated by using a computer programme SPSS/PEARSON CORRELATION (Nie et al., 1975).

3.5.3 Heritability estimates

Both the broad and narrow sense heritability estimates were calculated. The genetical components used were obtained as in Section 3.4.2.

(i) Narrow sense heritability (h_N^2)

$$h_N^2 = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E} \quad (\text{Mather and Jinks, 1971})$$

(ii) Broadsense heritability (h_B^2)

$$h_B^2 = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E} \quad (\text{Mather and Jinks, 1971})$$

3.5.4 Estimates of hybrid vigour

Hybrid vigour was estimated as per cent increase of F_1 hybrids above the midparental value (Poehlman, 1979).

$$\text{i.e. \% heterosis} = \frac{(\text{Hybrid X} - \text{midparental value})}{\text{midparental value}} \times 100$$

This estimate was based on the genotype mean across the three blocks. Significant deviation of F_1 hybrids from the midparental values was tested using LSD (Least Significant Difference) (Steel and Torrie, 1980).

$$\text{LSD} = t \times \text{Seod} (F_1 - \text{MP}) = t \times \sqrt{(\sigma_{F_1}^2/b) + (\sigma_{\text{MP}}^2/2b)}$$
 where $\sigma_{F_1}^2$ = error variance of hybrids, σ_{MP}^2 = error variance of midparents, b = number of replications and t =tabulated t value for error degree of freedom.

3.5.5 Correlation coefficients

Correlation coefficients (r) between traits X and Y can be estimated from:

$$r = \frac{\sum (X - \bar{X}) (Y - \bar{Y}) / (n - 1)}{\sqrt{(\sum (X - \bar{X})^2 / (n - 1))} \cdot \sqrt{(\sum (Y - \bar{Y})^2 / (n - 1))}}$$

(Steel and Torrie, 1980; Draper and Smith, 1981)

where $\sum (X - \bar{X}) (Y - \bar{Y}) / (n - 1) =$ covariance between trait X and Y (COV XY), $\sqrt{\sum (X - \bar{X})^2 / (n - 1)} =$ standard deviation of trait X (σ_X) and $\sqrt{\sum (Y - \bar{Y})^2 / (n - 1)} =$ standard deviation of trait Y (σ_Y).

Based on this, the phenotypic (r_p) and genotypic (r_g) correlation coefficients between traits X and Y were estimated by using the appropriate phenotypic, genotypic covariances and standard deviations respectively.

A computer programme PHANIE (Gordon, unpublished) was used.

Except for those stated where standard computer programmes were used, specific computer programmes were written to estimate V_r and W_r , second degree statistics (Section 3.5.2.2), estimates of genetical components (Section 3.5.2.3), and heritability estimates (Section 3.5.3). The listings of these programmes are presented in Appendices 2 and 3.

3.5.6 Symbols used to indicate the levels of significance.

The significance symbols used in this study were:

NS, not significant = $p > 0.10$

(NS) = $0.10 \geq p > 0.05$

* = $0.05 \geq p > 0.01$

** = $0.01 \geq p > 0.005$

*** = $0.005 \geq p > 0.001$

**** = $0.001 \geq p$

4. RESULTS AND ASSOCIATED DISCUSSION

4.1 PHENOTYPIC ANALYSIS

The full analyses of variance tables are presented in Appendix 4. For convenience however, the genotypic variance component estimates together with their standard errors, levels of significance and ratio to errors are presented in Table 4.1.

Genotypes were found to be significantly different for all characters and leaf positions except for wing area (2nd leaf). Genotypic variance to error ratios were also high (greater than 1) for most characters. This suggested that high genetic variability was present for the characters and genotypes studied. Therefore, except for wing area (2nd leaf), diallel analyses were warranted for other characters.

The genotypic means for all characters are presented in Appendix 5. Table 4.2 shows the grand mean (character mean) for each leaf position. The leaf ratio and differential index indicated that the upper leaves were narrower than the bottom leaves. Upper leaves also had more attenuated tips and narrower vein angles. Other characters such as petiole lengths, wing widths, auricle areas, leaf dry weights and leaf areas were also found to be lower in the top leaves. This is mainly due to the fact that a fully grown plant is generally pyrimidical in shape with the biggest leaf near the bottom and becoming smaller towards the top (Lapham, 1975).

4.2 DIALLEL ANALYSIS

The mean estimates of array variance (V_r), array

TABLE 4.1

GENOTYPIC VARIANCE COMPONENT ESTIMATES, THEIR STANDARD
ERRORS, LEVEL OF SIGNIFICANCES AND RATIO TO ERRORS

CHARACTERS	$\hat{\sigma}_G^2$	S.E.	SIG.	RATIO TO ERROR
1. LEAF RATIO				
a) 2nd leaf	6.2954	1.5970	****	3.74
b) 7th leaf	1.2955	0.3242	****	4.44
c) 12th leaf	0.6073	0.1503	****	5.27
d) 17th leaf	0.3083	0.0799	****	2.99
2. DIFFERENTIAL INDEX				
a) 2nd leaf	2.2836	0.6360	****	1.75
b) 7th leaf	0.6076	0.1970	****	0.90
c) 12th leaf	0.4023	0.1410	****	0.71
d) 17th leaf	0.2223	0.1181	*	0.29
3. RAPER'S INDEX I				
a) 2nd leaf	0.0290	0.0163	*	0.27
b) 7th leaf	0.1028	0.0342	****	0.83
c) 12th leaf	0.0254	0.0082	****	0.91
d) 17th leaf	0.0109	0.0047	***	0.44
4. RAPER'S INDEX II				
a) 2nd leaf	3.3440	0.8831	****	2.53
b) 7th leaf	5.6177	1.4691	****	2.75
c) 12th leaf	2.0933	0.6151	****	1.33
d) 17th leaf	2.5797	0.6731	****	2.80
5. TIP SCORE (NORMALISED)				
a) 2nd leaf	0.3052	0.0758	****	4.98
b) 7th leaf	0.3292	0.0813	****	5.49
c) 12th leaf	0.3136	0.0808	****	3.16
d) 17th leaf	0.2281	0.0611	****	2.25
6. PETIOLE LENGTH				
a) 2nd leaf	403.37	144.24	****	0.67
b) 7th leaf	620.76	155.78	****	4.28
c) 12th leaf	814.64	203.88	****	4.44
d) 17th leaf	551.67	147.57	****	2.29
7. WING WIDTH				
a) 2nd leaf	319.88	82.35	****	3.18
b) 7th leaf	427.52	104.11	****	7.10
c) 12th leaf	506.66	127.15	****	4.28
d) 17th leaf	413.73	105.07	****	3.69

TABLE 4.1 (Cont.)

CHARACTER	$\hat{\sigma}_G^2$	S.E.	SIG.	RATIO TO ERROR
8. WING AREA				
a) 2nd leaf	3.7326	3.4564	NS	0.13
b) 7th leaf	31.8452	13.1992	***	0.47
c) 12th leaf	71.7858	24.7453	****	0.74
d) 17th leaf	51.5595	19.6084	****	0.57
9. AURICLE AREA				
a) 2nd leaf	20.406	5.551	****	2.03
b) 7th leaf	107.455	27.081	****	4.05
c) 12th leaf	79.368	19.552	****	5.67
d) 17th leaf	40.684	10.282	****	3.91
10. VEIN ANGLE				
a) 2nd leaf	62.213	15.486	****	4.80
b) 7th leaf	88.551	21.812	****	5.69
c) 12th leaf	142.644	34.616	****	7.69
d) 17th leaf	117.899	28.827	****	6.53
11. LEAF DRY WEIGHT				
a) 2nd leaf	0.0349	0.0106	****	1.14
b) 7th leaf	0.1428	0.0469	****	0.87
c) 12th leaf	0.2936	0.0847	****	1.45
d) 17th leaf	0.0775	0.0308	****	0.52
12. LEAF AREA				
a) 2nd leaf	2053.38	710.67	****	0.74
b) 7th leaf	12046.53	3610.16	****	1.22
c) 12th leaf	32501.88	8612.85	****	2.46
d) 17th leaf	14440.90	4656.10	****	0.92

TABLE 4.2

GRAND MEAN FOR EACH LEAF POSITION

CHARACTER	2nd LEAF	7th LEAF	12th LEAF	17th LEAF
1. LEAF RATIO	5.15	3.39	2.87	2.43
2. DIFFERENTIAL INDEX	3.60	3.82	4.02	4.64
3. RAPER'S INDEX I	2.47	2.16	2.05	2.04
4. RAPER'S INDEX II	3.80	3.84	3.89	4.71
5. TIP SCORE (NORMALISED)	3.67	3.28	3.26	3.03
6. PETIOLE LENGTH (mm)	39.78	70.69	98.80	104.05
7. WING WIDTH (mm)	25.93	40.16	35.73	37.12
8. WING AREA (cm ³)	11.42	35.78	43.19	46.09
9. AURICLE AREA (cm ³)	3.14	11.89	7.80	7.41
10. VEIN ANGLE (degrees)	33.84	44.92	47.23	49.57
11. LEAF DRY WEIGHT (g)	0.5126	1.7563	1.9952	2.0580
12. LEAF AREA (cm ³)	124.41	407.74	607.75	704.53

parent-offspring covariance (W_r), ($W_r + V_r$) and ($W_r - V_r$) for both the 8 x 8 original data and 7 x 7 reanalysed data are presented in Appendix 6. The estimates of second degree statistics are presented in Appendix 7.

The diallel results here are presented character by character. For each character, the statistics for the test of the additive-dominance model, (W_r, V_r) regression statistics, ($(W_r + V_r), \bar{P}$) correlation coefficients and genetical component estimates, including their ratios are presented in a table. The (W_r, V_r) graphs are also presented. Where reduced data sets were analysed to investigate epistasis and/or gene association, these statistics are given as well.

4.2.1 Leaf ratio

All the diallel statistics for leaf ratio are presented in Table 4.3.

Except for the 7th leaf, the ($W_r - V_r$) were found to be heterogeneous. Regression coefficients ($\hat{b}_1$) were also significant from unity. An overall view suggested that inter-locus interaction was probably present for leaf ratio. The ($W_r + V_r$) which were heterogeneous indicated that dominance was present.

Additive genetic variance ($\hat{D}$) was greater than the dominance genetic variance ($\hat{H}_1$ and $\hat{H}_2$) for 7th, 12th and 17th leaves. In the case of 2nd leaf, dominance genetic variance was greater. Both estimates of genetical variance increased steadily from the bottom to the top leaves.

TABLE 4.3 LEAF RATIO

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS, AND (D) GENETICAL COMPONENTS ESTIMATES.

ANALYSIS		2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSIS OF VARIANCE OF W_r AND V_r :					
($W_r + V_r$):	df				
Array Differences	7	85.32*	1.47NS	0.403***	0.324***
Error	14	35.37	0.82	0.042	0.058
($W_r - V_r$):					
Array Differences	7	43.71*	0.44NS	0.056*	0.030*
Error	14	10.35	0.34	0.015	0.009
(B) (W_r , V_r) REGRESSION STATISTICS:					
W_r Intercept ($\hat{b}_0$)		2.41	0.68	0.29	0.12
Regression Coefficient ($\hat{b}_1$)		0.15	0.32	0.42	0.56
Std. Error Of $\hat{b}_1$		0.054	0.045	0.075	0.052
t - test ($\hat{b}_1 = 0$)		2.82**	7.29***	5.57***	10.72***
t - test ($\hat{b}_1 = 1$)		15.54***	15.16***	7.85***	8.41***
Coefficient of determination (R^2)		0.27	0.71	0.59	0.84
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:					
Correlation Coefficient ($\hat{r}$)		0.37*	0.54***	0.77***	0.70****
(D) GENETICAL COMPONENTS:					
$\hat{D}$		3.94	1.35	0.75	0.50
$\hat{H}_1$		9.12	0.53	0.29	0.13
$\hat{H}_2$		6.62	0.66	0.23	0.18
$\hat{F}$		-4.67	-1.26	-0.37	-0.08
$\hat{E}$		1.68	0.29	0.12	0.10
$\sqrt{(H_1/D)}$		1.52	0.63	0.62	0.51
$H_1/4H_2 (=UV)$		0.18	0.31	0.20	0.34
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$		-0.75	-1.55	-0.88	-0.26
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$					
$= K_D/K_R$		0.44	0.15	0.43	0.74

The degree of dominance ($\sqrt{\hat{H}_1/\hat{D}}$) indicated that partial dominance was present except for the 2nd leaf where overdominance was observed. The proportions of positive to negative alleles were approximately equal in the 12th leaf ($\overline{UV} \approx 0.25$) but not for other leaf positions. The $\frac{1}{2}\hat{F}/\sqrt{\hat{D}} (\hat{H}_1 - \hat{H}_2)$ ratios were found to be approximately equal to 1 for 2nd and 12th leaves. This suggested that the observed partial or overdominance was consistent for all the loci (rather than variable degrees of dominance at different loci, including no dominance). The K_D/K_R ratio and $\hat{F}$ value indicated that more recessive alleles were present for all the leaf positions.

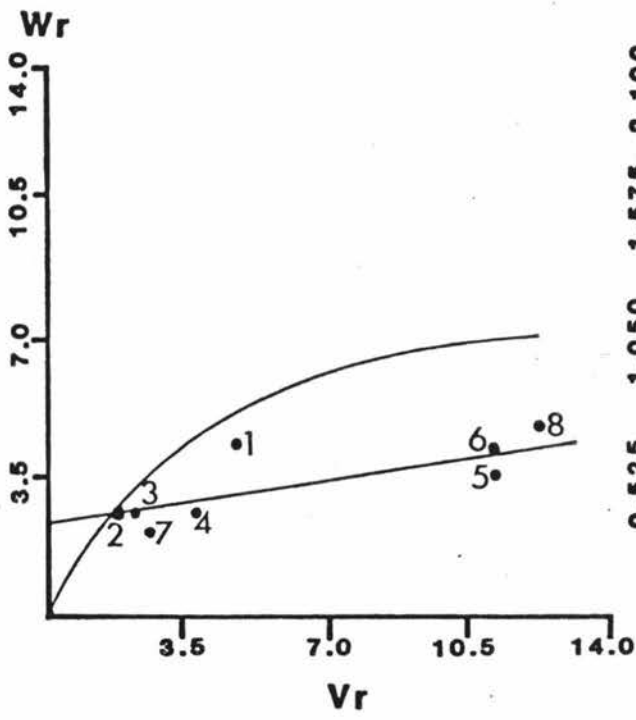
The graphic analysis (Figure 4.1) showed that parents 8, 6 and 5 contained most recessive alleles, while parents 2 and 3 contained most dominant alleles.

The $((W_r + V_r), \bar{P})$ correlation coefficients were positive and highly significant, indicating that wider leaves were dominant to narrower leaves.

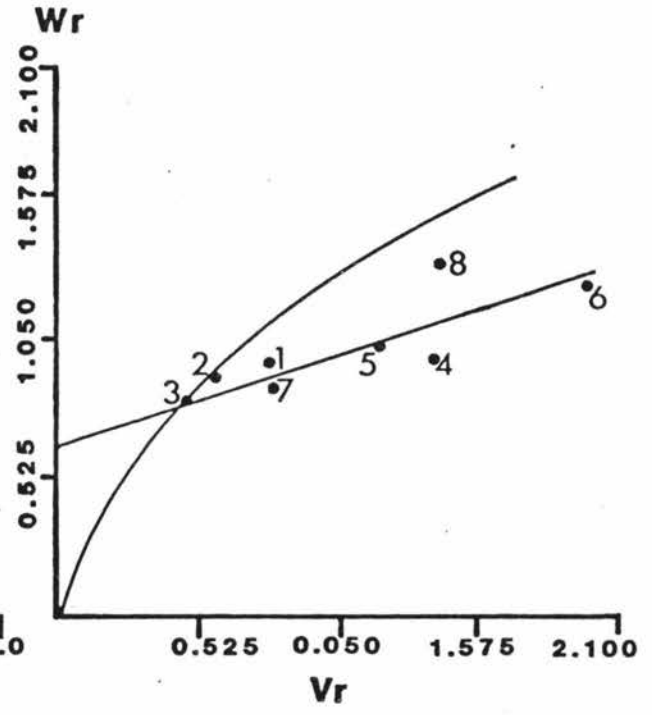
4.2.2 Differential index

The diallel statistics for differential index are presented in Table 4.4.

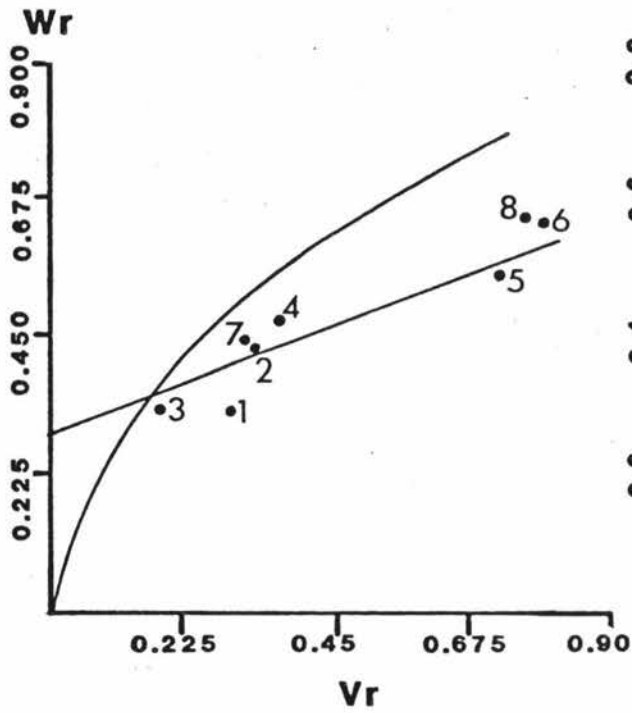
The analysis of variance of $(W_r + V_r)$ was significant only for 2nd leaf. This generally indicated that dominance was of little importance for this character. None of $(W_r - V_r)$ analyses of variance were found to



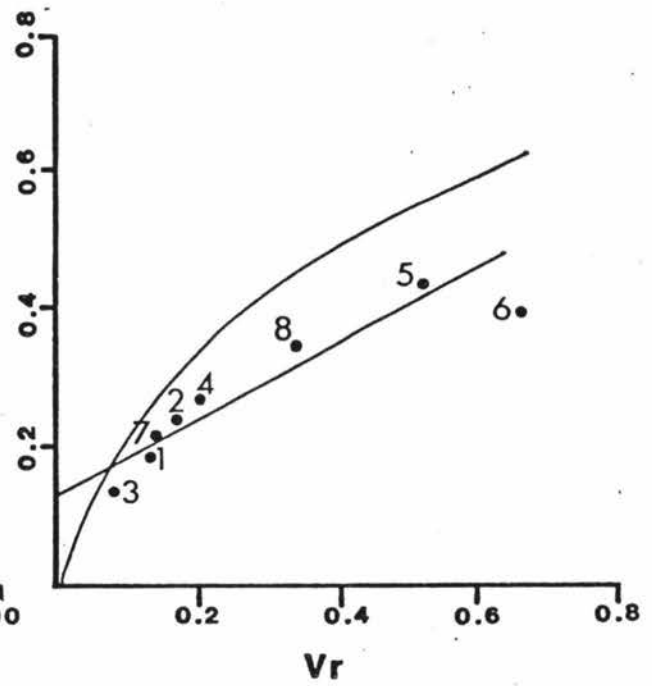
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



(d) 17th LEAF

FIGURE 4.1 (W_r , V_r) GRAPHS FOR LEAF RATIO

TABLE 4.4 DIFFERENTIAL INDEX

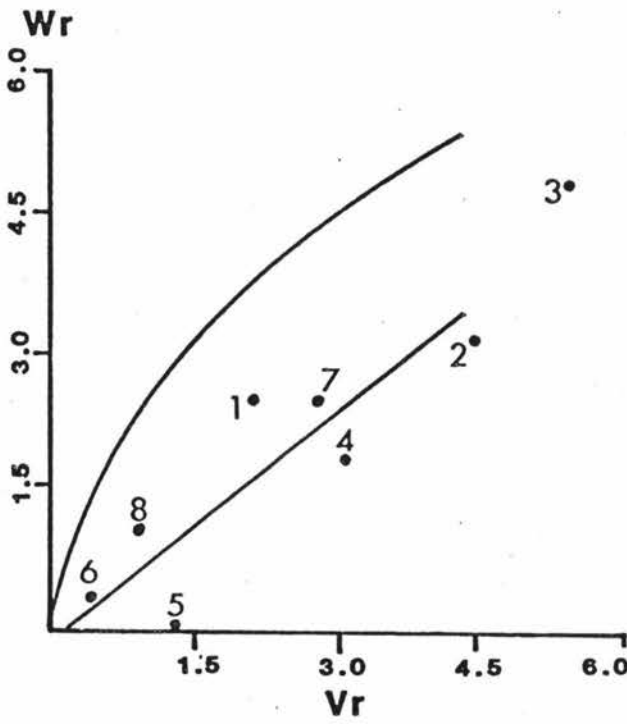
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r, V_r) REGRESSION STATISTICS, (C) $((W_r + V_r), \bar{P})$ CORRELATION
 COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS	2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :				
$(W_r + V_r)$ df				
Array Differences 7	31.29*	1.29NS	1.58NS	0.39NS
Error 14	7.99	0.74	1.63	1.12
$(W_r - V_r)$				
Array Differences 7	1.52NS	0.41NS	0.22NS	0.22NS
Error 14	1.33	0.20	0.22	0.12
(B) (W_r, V_r) REGRESSION STATISTICS:				
W_r Intercept ($\hat{b}_0$)	0.09	0.08	0.02	0.30
Regression Coefficient ($\hat{b}_1$)	0.83	0.65	0.74	0.55
Std. Error Of $\hat{b}_1$	0.139	0.240	0.129	0.113
t - test ($\hat{b}_1 = 0$)	5.97***	2.72*	5.72***	4.83***
t - test ($\hat{b}_1 = 1$)	1.22 NS	1.44 NS	2.02 NS	3.98***
Coefficient of determination (R^2)	0.62	0.25	0.60	0.53
(C) $((W_r + V_r), \bar{P})$ CORRELATION:				
Correlation Coefficient ($\hat{r}$)	0.64****	0.28NS	0.73****	0.51**
(D) GENETICAL COMPONENTS:				
$\hat{D}$	5.54	1.10	1.34	0.32
$\hat{H}_1$	3.06	0.49	0.20	0.48
$\hat{H}_2$	1.78	0.88	0.24	0.68
$\hat{F}$	3.59	0.06	0.89	0.23
$\hat{E}$	1.30	0.67	0.57	0.76
$\sqrt{(H_1/D)}$	0.74	0.67	0.38	1.22
$H_1/4H_2 (=UV)$	0.15	0.45	0.30	0.35
$\frac{1}{2}\sqrt{D(H_1 - H_2)}$	-0.67	0.05	1.87	0.46
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$				
$= K_D/K_R$	2.55	1.08	13.81	1.85

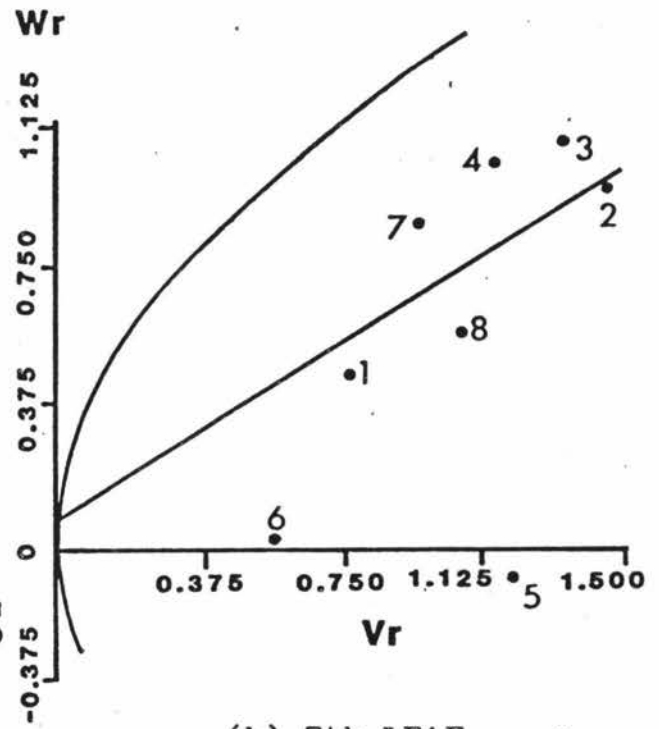
be significant. The deviation of $\hat{b}_1$ from unity were not significant except for 17th leaf. This strongly suggested that this character do follow the additive-dominance model. In the absence of inter-locus interaction and very little dominance (homogeneous ($W_r + V_r$)), additive genetic variance was probably the principal component of genetic variance.

The genetical variance components estimates showed that additive genetic variance ($\hat{D}$) was higher than the dominance genetic variance ($\hat{H}_1$ and $\hat{H}_2$) for all leaf positions. These observations agreed with the significant ($W_r + V_r$) analyses of variance. When compared across the leaf positions, both the dominance and additive genetic variances were higher in the upper leaves as compared to the bottom leaves. The $\sqrt{\hat{H}_1/\hat{D}}$ values indicated that partial dominance were observed for all the leaf positions. The $\frac{1}{2}\hat{F}/\sqrt{\hat{D}(\hat{H}_1 - \hat{H}_2)}$ indicated that the observed partial dominance was not consistently distributed across all the loci. The UV values indicated that the positive and negative alleles were present in equal proportions only for the 7th leaf. Consistent results were obtained from the F and K_D/K_R values. Dominant alleles were more prominent in 2nd, 12th and 17th leaves.

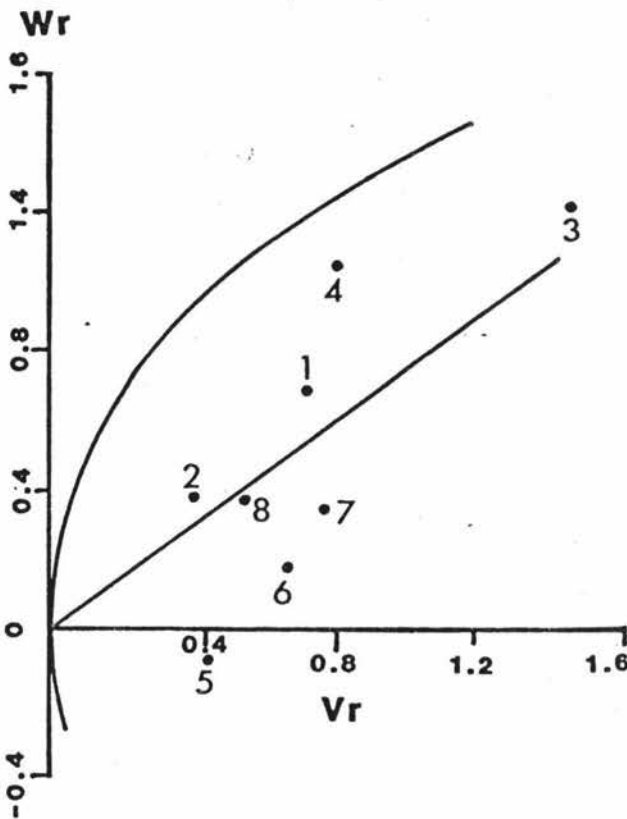
The (W_r, V_r) graphs (Figure 4.2) indicated that parents 2 and 3 contained more dominant alleles, while parents 5 and 6 contained most of the recessive alleles for all the leaf positions.



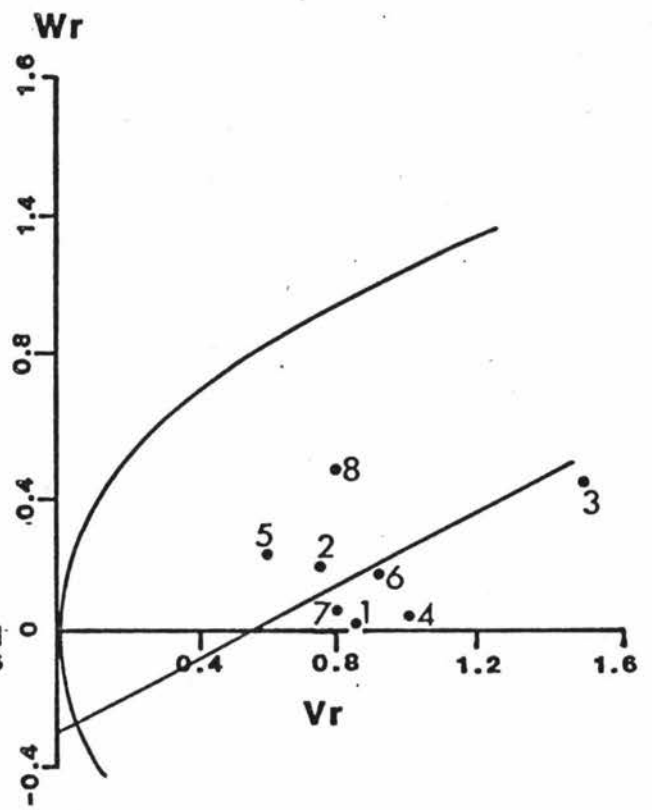
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



(d) 17th LEAF

FIGURE 4.2 (W_r , V_r) GRAPHS FOR DIFFERENTIAL INDEX

The $((Wr + Vr), \bar{P})$ correlation coefficients were positive and highly significant for the 2nd, 12th and 17th leaves. This generally showed that narrow leaves were dominant to the broader leaves.

4.2.3 Raper's index I

Table 4.5 shows the diallel statistics obtained for Raper's index I.

The $(Wr + Vr)$ were homogeneous except for the 7th leaf. This generally showed that dominance was trivial for this character. Homogeneity of $(Wr - Vr)$ were observed for all the leaf positions. $\hat{b}_1$ were not significant for 2nd and 12th leaves. In the case of 7th and 17th leaves, even though the deviations $\hat{b}_1$ from unity were significant, the R^2 of the (Wr, Vr) regressions were low. Thus the validity of this test was doubtful. Therefore inter-locus interaction was probably trivial for this character.

Even though both the dominance ($\hat{H}_1$ and $\hat{H}_2$) and additive ($\hat{D}$) genetic variances were relatively small as compared to the error variances, the additive genetic variance was still higher than the dominance genetic variances. The $\sqrt{\hat{H}_1/\hat{D}}$ indicated that partial dominance was present in all the leaf positions. This is consistent with the non-significant $(Wr + Vr)$ analyses of variance. Except for the 7th leaf, the observed dominance were not consistently distributed across the loci. The $\overline{UV}$ values indicated

TABLE 4.5 RAPER'S INDEX I

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS					
(A) MEAN SQUARES OF THE ANALYSIS OF VARIANCE OF W_r AND V_r :					
($W_r + V_r$):	df				
Array Differences	7	0.0099NS	0.4541***	0.0016NS	0.00074NS
Error	14	0.0164	0.0873	0.0019	0.00064
($W_r - V_r$):					
Array Differences	7	0.0124NS	0.0550NS	0.0012NS	0.00021NS
Error	14	0.0109	0.0431	0.0013	0.00029
(B) (W_r , V_r) REGRESSION STATISTICS:					
W_r Intercept ($\hat{b}_0$)		0.0425	0.0150	0.0264	0.0020
Regression Coefficient ($\hat{b}_1$)		0.13	0.43	0.05	0.38
Std. Error Of $\hat{b}_1$		0.159	0.112	0.129	0.174
t - test ($\hat{b}_1 = 0$)		0.83 NS	3.81***	0.35NS	2.16*
t - test ($\hat{b}_1 = 1$)		5.44***	5.15***	7.34***	3.59**
Coefficient of determination (R^2)		0.03	0.41	0.01	0.17
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:					
Correlation Coefficient ($\hat{r}$)		0.35*	0.70****	0.13NS	0.06NS
(D) GENETICAL COMPONENTS:					
$\hat{D}$		0.128	0.445	0.048	0.022
$\hat{H}_1$		-0.010	0.352	0.005	0.022
$\hat{H}_2$		0.039	0.169	0.019	0.019
$\hat{F}$		0.077	0.594	-0.004	0.016
$\hat{E}$		0.109	0.124	0.028	0.025
$\sqrt{(H_1/D)}$		0.291	0.889	0.325	0.994
$H_1/4H_2 (=UV)$		-0.896	0.119	0.956	0.224
$\frac{1}{2}F/\sqrt{(D(H_1 - H_2))}$		0.483	1.038	-0.082	1.148
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ = K_D/K_R		-58.896	7.013	0.757	2.176

that the positive and negative alleles were unequally present. The K_D/K_R ratios and $\hat{F}$ values showed that more dominant alleles were present for 2nd, 7th and 17th leaves. More recessive alleles were present for the 12th leaf.

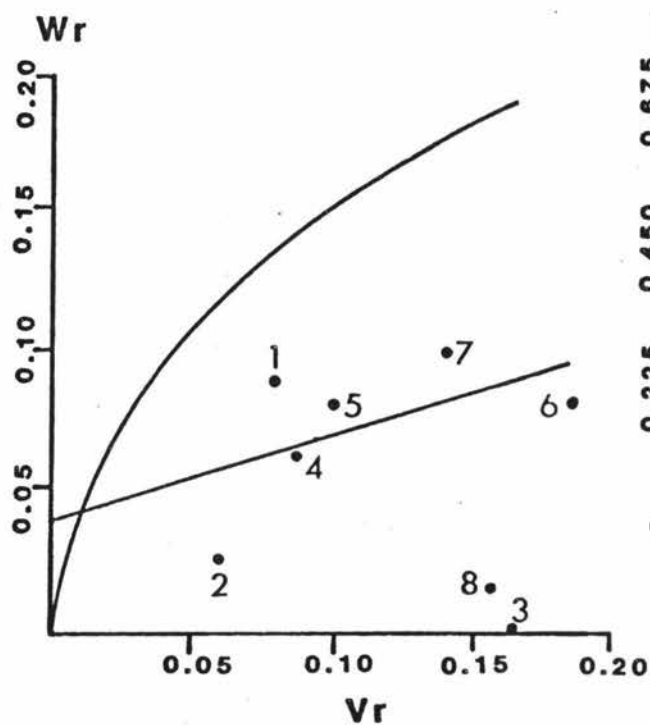
The (Wr, Vr) regression graphs are shown in Figure 4.3. Except for the 7th leaf, the (Wr, Vr) points were found to cluster together and thus there was no clear cut distribution of the parents with respect to those containing most dominant or recessive alleles. However an overall view indicated that parents 4 and 6 had the most recessive alleles for all the leaf positions. The parents which have the most dominant alleles were found to be inconsistent across the leaf positions.

The ((Wr + Vr), $\bar{P}$) correlation coefficients were positive for all the leaf positions. These coefficients were significant for the 2nd and 7th leaves. This suggested that the leaves with the point of widest section nearer to the tips (i.e. smaller indices) were controlled by the dominant genes.

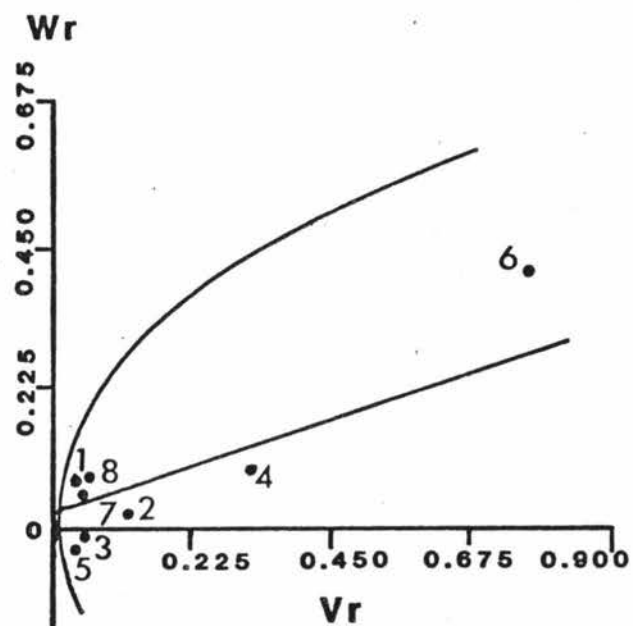
4.2.4 Raper's index II

The diallel statistics obtained for Raper's index II are presented in Table 4.6.

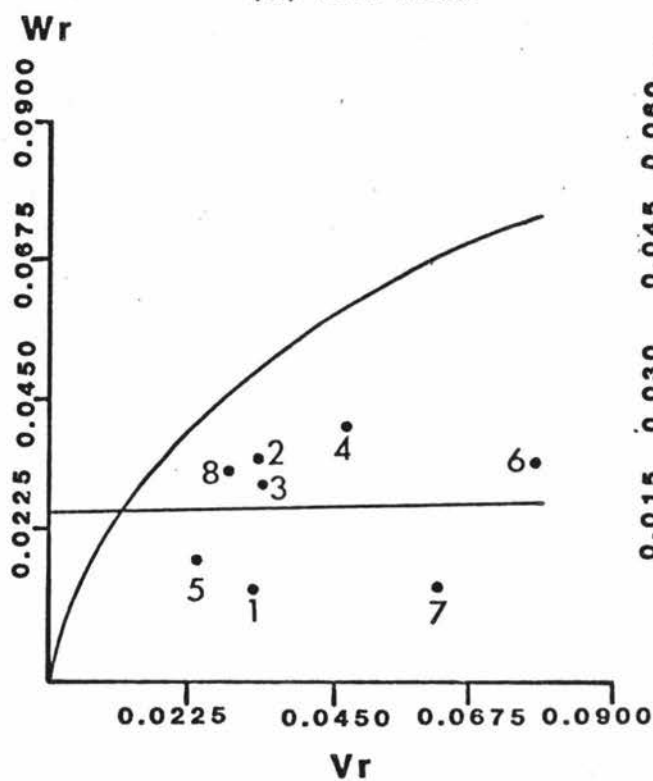
The (Wr + Vr) analyses of variance which were



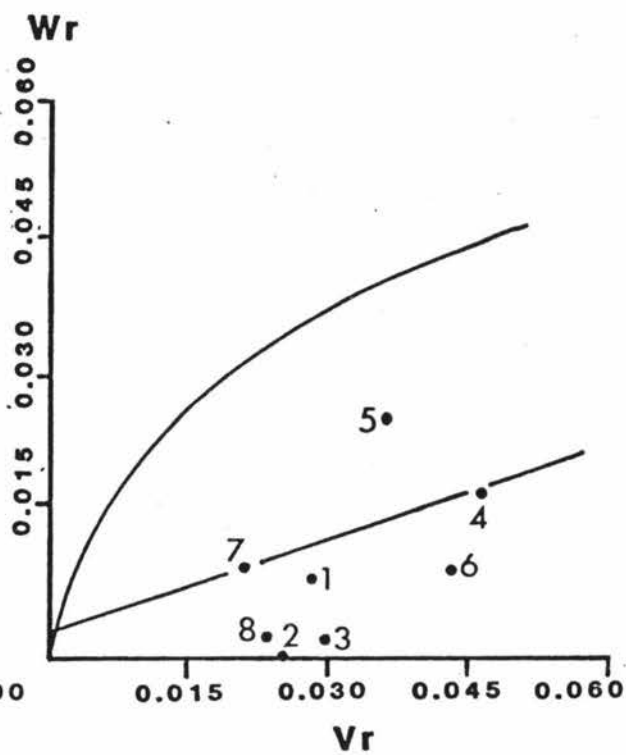
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



(d) 17th LEAF

FIGURE 4.3 (W_r , V_r) GRAPHS FOR RAPER'S INDEX I

TABLE 4.6 RAPER'S INDEX II

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS, AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS		2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r and V_r :					
($W_r + V_r$):	df				
Array Differences	7	26.41**	235.88***	103.65*	59.25***
Error	14	5.80	33.55	31.27	10.30
($W_r - V_r$)					
Array Differences	7	3.11	33.29***	5.13NS	14.64**
Error	14	2.11	4.57	4.58	3.39
(B) (W_r , V_r) REGRESSION STATISTICS:					
W_r Intercept ($\hat{b}_0$)		0.27	0.27	0.16	0.65
Regression Coefficient ($\hat{b}_1$)		0.60	0.55	0.68	0.37
Std. Error of $\hat{b}_1$		0.081	0.081	0.076	0.37
t - test ($\hat{b}_1 = 0$)		4.14***	6.86***	8.95***	3.93***
t - test ($\hat{b}_1 = 1$)		2.82**	5.52***	4.26***	6.79***
Coefficient of determination (R^2)		0.44	0.68	0.78	0.41
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:					
Correlation Coefficient ($\hat{r}$)		0.39*	0.51**	0.74****	0.22NS
(D) GENETICAL COMPONENTS:					
$\hat{D}$		4.819	6.901	6.126	4.846
$\hat{H}_1$		4.949	9.662	3.481	6.351
$\hat{H}_2$		4.725	9.543	2.767	5.534
$\hat{F}$		0.602	0.120	5.017	3.356
$\hat{E}$		1.324	2.046	1.577	0.921
$\sqrt{(H_1/D)}$		1.014	1.183	0.754	1.145
$H_1/4H_2 (=UV)$		0.239	0.247	0.199	0.218
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$		0.289	0.066	1.199	0.843
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ = K_D/K_R		1.131	1.015	3.378	1.867

significant for all leaf positions indicated that dominance is important for this character. The ($W_r - V_r$) were heterogeneous for the 7th and 17th leaves. Deviations of $\hat{b}_1$ from unity were found to be significant for all the leaf positions. Therefore an overall view indicated that inter-locus interaction was probably present for this character.

Except for the 12th leaf, dominance genetic variances ($\hat{H}_1$ and $\hat{H}_2$) were generally greater than the additive genetic variance ($\hat{D}$). This was consistent with the highly significant ($W_r + V_r$) analysis of variance. Additive genetic variance was higher for the middle leaves as compared to other leaf positions. On the other hand dominance genetic variances were higher in the upper as compared to the bottom leaves. Except for the 12th leaf, overdominance was observed for other leaf positions. Partial dominance was found to be present for the 12th leaf. The $\frac{1}{2}\hat{F}/\sqrt{\hat{D}} (\hat{H}_1 - \hat{H}_2)$ ratio indicated the observed dominance was consistently distributed across the loci only for the 12th and 17th leaves. The $\overline{UV}$ values which was approximately 0.25 for the 2nd and 7th leaves indicated that the positive and negative alleles were present in equal proportions in these leaf positions. Consistent results were obtained from K_D/K_R and $\hat{F}$ values. Both statistics indicated that the proportions of dominant and recessive alleles were approximately equal for the 2nd and 7th leaves. More dominant alleles were present for the 12th and

17th leaves.

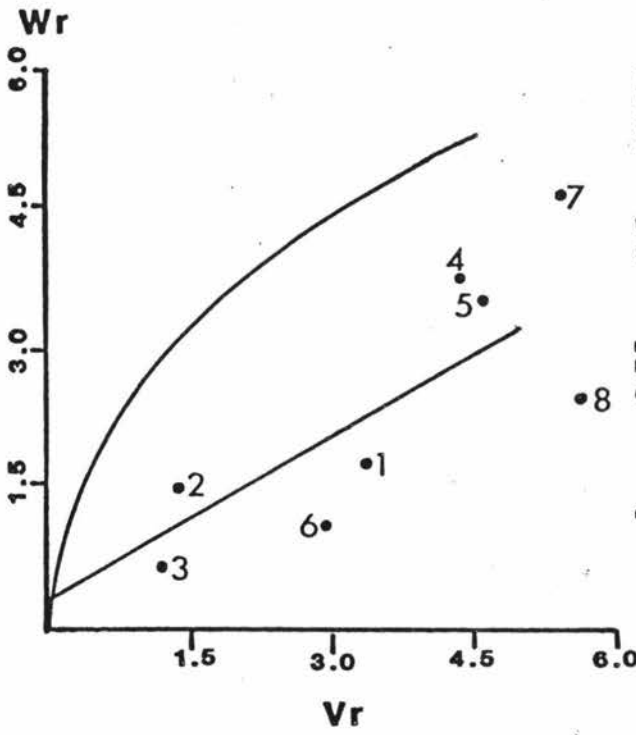
The (Wr, Vr) graphs are shown in Figure 4.4. Parents 5, 6 and 8 were generally found to have the most recessive alleles. On the other hand, parents 2, 3 and 7 were generally found to have the most dominant alleles.

The ((Wr + Vr), $\bar{P}$) correlation coefficients were positive for all the leaf positions. The coefficients were all significant, except for the 17th leaf. An overall view therefore indicated that the smaller index (i.e. relatively wider auricle width in relation to lamina width) was controlled by the dominant genes.

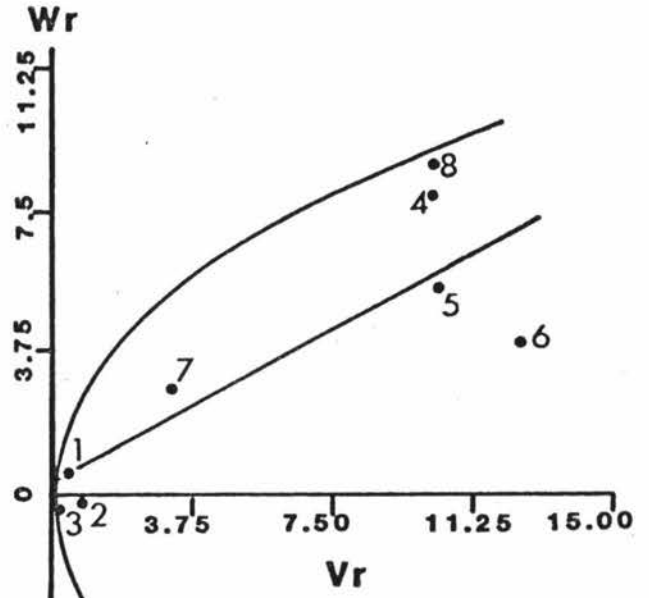
4.2.5 Tip Score

All the diallel statistics for tip score are presented in Table 4.7.

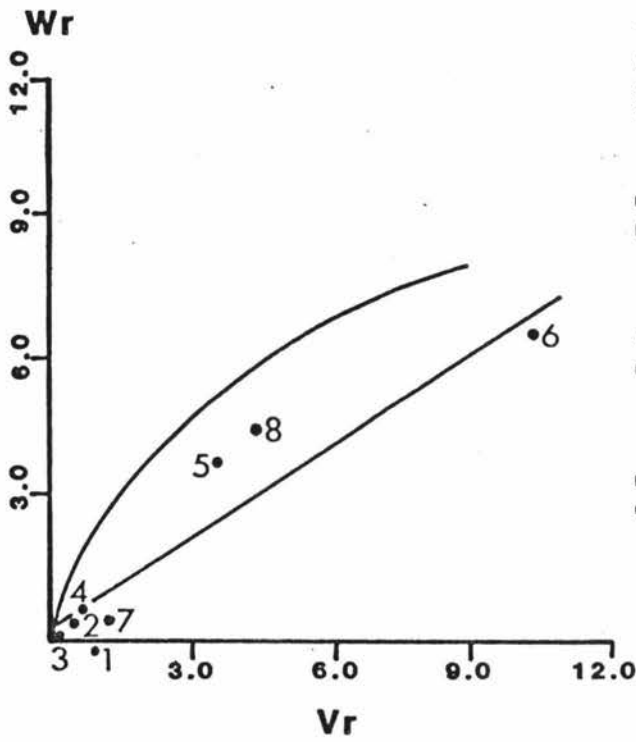
The (Wr + Vr) were found to be heterogeneous in all the leaf positions. This showed that dominance was important for this character. The importance of dominance was also shown by the distribution of the (Wr, Vr) points along the regression lines (Figure 4.5) and good R^2 values. The (Wr - Vr) were homogeneous except for the 2nd leaf. Test of significance of $\hat{b}_1$ from unity was also found to be significant only for 2nd and 12th leaves. Thus there was strong indication that inter-locus interactions were absent except for the 2nd leaf. Even then, the (Wr - Vr) analysis of variance which was



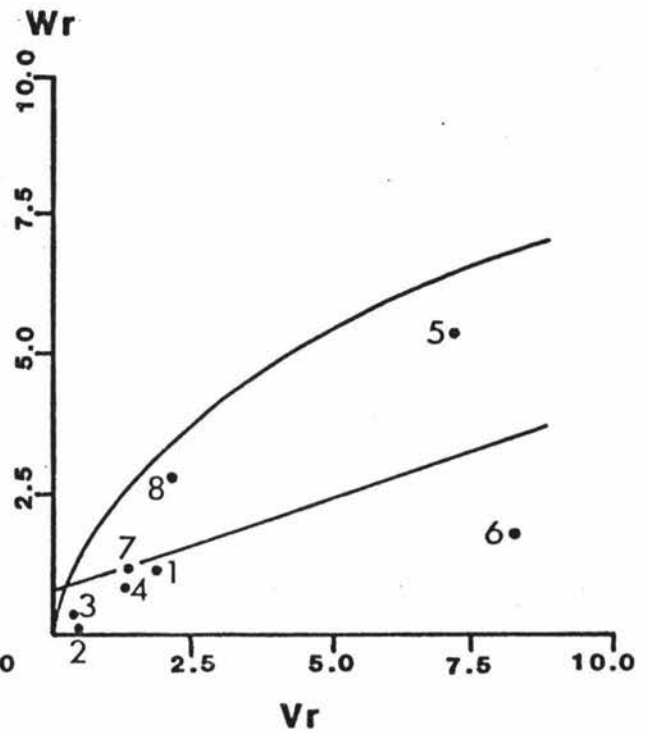
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



(d) 17th LEAF

FIGURE 4.4 (W_r , V_r) GRAPHS FOR RAPER'S INDEX II

TABLE 4.7 TIP SCORE

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

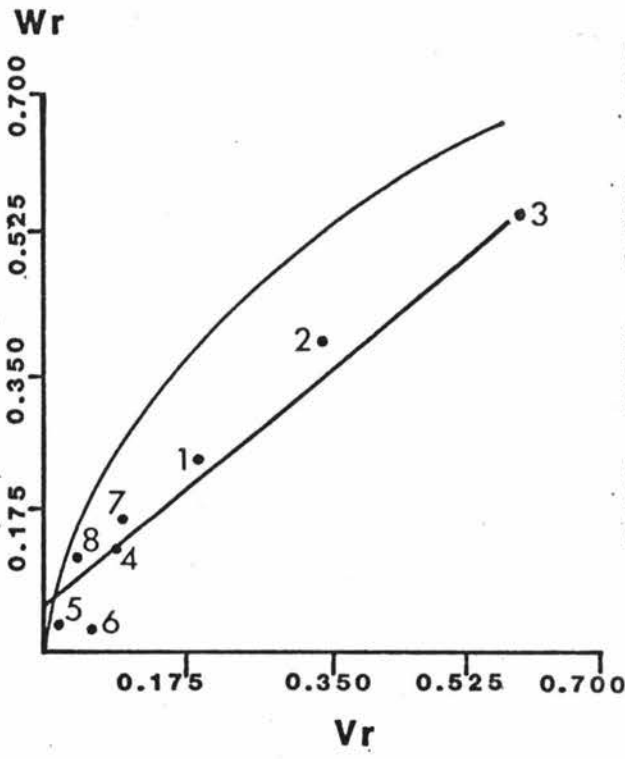
ANALYSIS		2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :					
($W_r + V_r$):	df				
Array Differences	7	0.01271***	0.1497***	0.1737*	0.0791*
Error	14	0.1534	0.0167	0.0304	0.0211
($W_r - V_r$):					
Array Differences	7	0.0056*	0.0015NS	0.00289NS	0.0029NS
Error	14	0.0026	0.1156	0.00183	0.0025
(B) (W_r , V_r) REGRESSION STATISTICS:					
W_r Intercept ($\hat{b}_0$)		0.05	0.08	0.10	0.04
Regression Coefficient ($\hat{b}_1$)		0.89	0.96	0.85	0.81
Std. Error Of $\hat{b}_1$		0.047	0.075	0.069	0.157
t - test ($\hat{b}_1 = 0$)		18.96***	12.88***	12.34***	5.15***
t - test ($\hat{b}_1 = 1$)		3.73**	0.43NS	2.21*	1.22NS
Coefficient of determination (R^2)		0.94	0.88	0.87	0.55
(C) (($W_r + V_r$), $\bar{P}$) CORRELATION:					
Correlation Coefficient ($\hat{r}$)		0.93****	0.81****	0.83****	0.65****
(D) GENETICAL COMPONENTS:					
$\hat{D}$		0.552	0.601	0.548	0.400
$\hat{H}_1$		0.205	0.064	-0.067	0.054
$\hat{H}_2$		0.152	0.077	-0.011	0.092
$\hat{F}$		0.306	0.117	0.016	-0.022
$\hat{E}$		0.061	0.060	0.099	0.101
$\sqrt{(H_1/D)}$		0.609	0.326	0.349	0.367
$H_1/4H_2 (=UV)$		0.185	0.303	0.0 0	0.427
$\frac{1}{2}F/\sqrt{D(H_1-H_2)}$		0.892	0.649	0.046	-0.091
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ $= K_D/K_R$		2.669	1.853	1.088	0.857

significant only at $p = 0.05$ for 2nd leaf. This suggested that the presence of inter-locus interaction was not very serious.

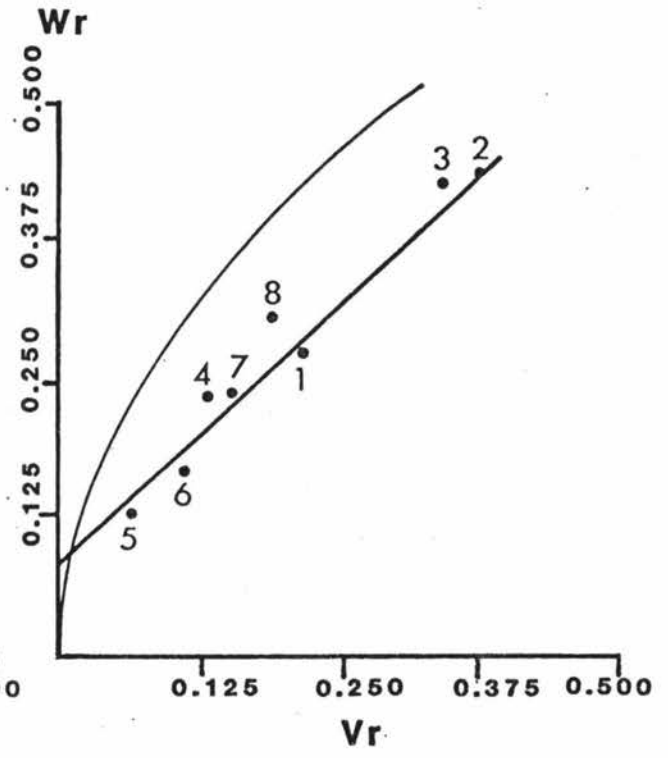
The additive genetic variance ($\hat{D}$) was generally higher than the dominance genetic variances ($\hat{H}_1$ and $\hat{H}_2$) for all leaf positions. Both the additive and dominance genetic variances were higher in the upper leaves as compared to the bottom leaves. The $\sqrt{\hat{H}_1/\hat{D}}$ values indicated that partial dominance was observed for all leaf positions. Also, the values were higher in the upper leaves. This was supported by the more heterogeneous ($W_r + V_r$) in the upper leaves. The $\frac{1}{2}\hat{F}/\sqrt{\hat{D}(\hat{H}_1 - \hat{H}_2)}$ indicated that the observed partial dominance was consistent across all the loci for the 2nd and 7th leaves but not for other leaf positions. The positive and negative alleles as shown by $\overline{UV}$ values were not present in equal proportions for 2nd and 17th leaves. The K_D/K_R ratios and $\hat{F}$ values indicated that more dominant genes were present for the 2nd, 7th and 12th leaves. The recessive alleles were found to be more for the 17th leaf.

For all the leaf positions, parents 1, 2 and 3 contained most of the recessive alleles (Figure 4.5). Parents 5 and 6 on the other hand contained most of the dominant alleles. The distribution of the parental points along the regression lines were consistent for all the leaf positions.

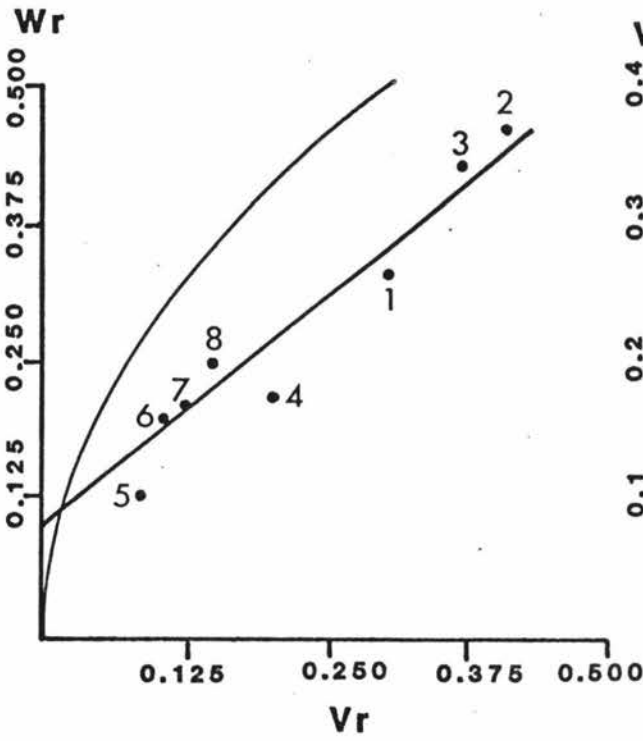
The correlation coefficients between ($W_r + V_r$) and $\bar{P}$ were negative and significant for all the leaf positions. This showed that the narrower and more attenuated tips were dominant to the broader and more



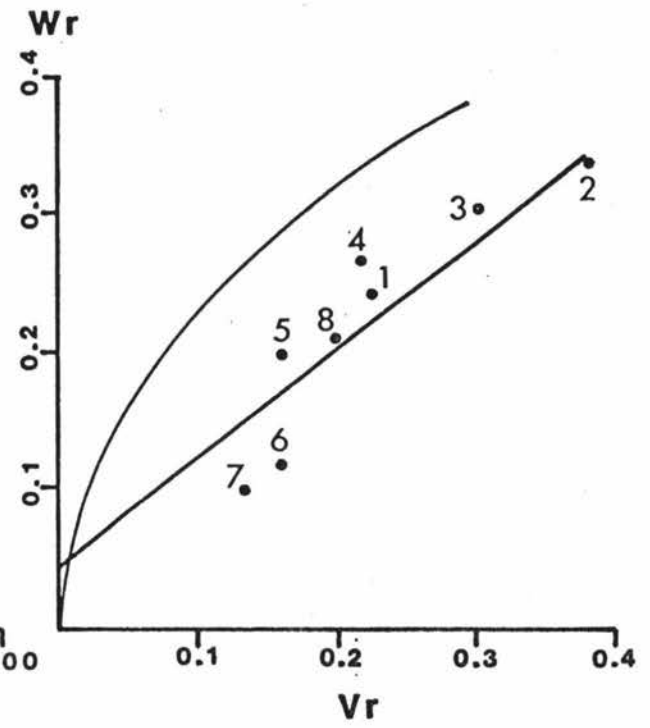
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



(d) 17th LEAF

FIGURE 4.5 (W_r , V_r) GRAPHS FOR TIP SCORE

rounded tips.

4.2.6 Petiole length

The diallel statistics obtained for petiole length are shown in Table 4.8.

The $(W_r + V_r)$ analyses of variance were significant only for the 12th and 17th leaves. This indicated that the non-additive genetic variance was less important for 2nd and 7th as compared to the 12th and 17th leaves. The analysis of $(W_r - V_r)$ was significant only for the 7th leaf ($p = 0.05$). Deviations of $\hat{b}_1$ from unity are not significant for 7th, 12th and 17th leaves. In the case of 2nd leaf, $\hat{b}_1$ was not significant. This was supported by the low R^2 (0.14) obtained. An overall view therefore suggested that inter-locus interaction was trivial for this character.

The additive genetic variances ($\hat{D}$) were greater than dominance genetic variance ($\hat{H}_1$ and $\hat{H}_2$) for all the leaf positions. The presence of higher additive genetic variance was more prominent in the top leaf (2nd leaf) as compared to other leaf positions. Both the components of genetic variance were higher in the middle leaves as compared to the top or bottom leaves. Based on $\sqrt{\hat{H}_1/\hat{D}}$, partial dominance was observed for all the leaf positions.

The $\frac{1}{2}\hat{F}/\sqrt{\hat{D}(\hat{H}_1 - \hat{H}_2)}$ indicated that the observed dominance was consistently distributed across all the loci for the 7th and 12th leaves, but not for the 2nd and 17th leaves. The $\overline{UV}$ values indicated that the negative and positive alleles were not present in

TABLE 4.8 PETIOLE LENGTH

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENT AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS		2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :		$\times 10^4$	$\times 10^4$	$\times 10^4$	$\times 10^4$
($W_r + V_r$):	df				
Array Differences	7	273.60NS	37.34NS	62.89***	35.30*
Error	14	271.10	14.78	6.20	84.24
($W_r - V_r$):					
Array Differences	7	167.40NS	5.10	1.96NS	3.33N
Error	14	173.10	1.79	4.39	2.60
(B) (W_r , V_r) REGRESSION STATISTICS:					
W_r Intercept ($\hat{b}_0$)		414.0	181.0	333.0	198.10
Regression Coefficient ($\hat{b}_1$)		0.10	0.99	0.82	0.72
Std. Error of $\hat{b}_1$		0.052	0.107	0.149	0.180
t - test ($\hat{b}_1 = 0$)		1.68NS	5.92***	5.49***	4.00
t - test ($\hat{b}_1 = 1$)		17.34***	0.09NS	1.20NS	1.56NS
Coefficient of determination (R^2)		0.14	0.61	0.58	0.42
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:					
Correlation Coefficient ($\hat{r}$)		0.27NS	0.002NS	-0.45**	-0.54**
(D) GENETICAL COMPONENTS:					
$\hat{D}$		825.19	1596.54	1791.77	1083.58
$\hat{H}_1$		-92.96	391.02	248.78	26.82
$\hat{H}_2$		138.88	266.90	273.31	124.55
$\hat{F}$		-19.82	712.83	355.36	8.68
$\hat{E}$		600.56	145.11	183.59	241.31
$\sqrt{(H_1/D)}$		0.336	0.495	0.373	0.158
$H_1/4H_2 (=UV)$		-0.374	0.171	0.275	1.161
$\frac{1}{2}\sqrt{D(H_1 - H_2)}$		-0.023	0.800	0.848	0.013
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ = K_D/K_R		0.931	2.644	1.725	1.052

equal proportions for all the leaf positions. The $\hat{F}$ and K_D/K_R values showed that more dominant alleles were present in the 7th, 12th and 17th leaves. More recessive alleles were however present in the 2nd leaf.

The (Wr, Vr) graphs are shown in Figure 4.6. Except for the 2nd leaf, parents 2 and 3 were found to contain most of the recessive alleles. Parents 5, 7 and 8 on the otherhand contained most of the dominant alleles. Parents 2, 3 and 7 were shown to contain most of the dominant alleles for the 2nd leaf.

The ((Wr + Vr), $\bar{P}$) correlation coefficients were negative and highly significant for the 12th and 17th leaves. An overall view therefore indicated that the dominant genes were responsible for the longer petiole.

4.2.7 Wing width

The diallel statistics for the original data are presented in Table 4.9.1.

Highly significant (Wr + Vr) analyses of variance were observed except for the 17th leaf. Thus generally there was strong evidence of dominance for this character. The (Wr-Vr) analyses were not significant for any leaf positions. Non-significant deviations of $\hat{b}_1$ from unity were observed for the 2nd, 7th and 17th leaves. Even though the deviation of $\hat{b}_1$ from unity was significant for 12th leaf, an overall view from both tests indicated that inter-locus interaction was of minor importance for this character.

Additive genetic variance estimates ($\hat{D}$) were found to be more predominance for all the leaf positions. This

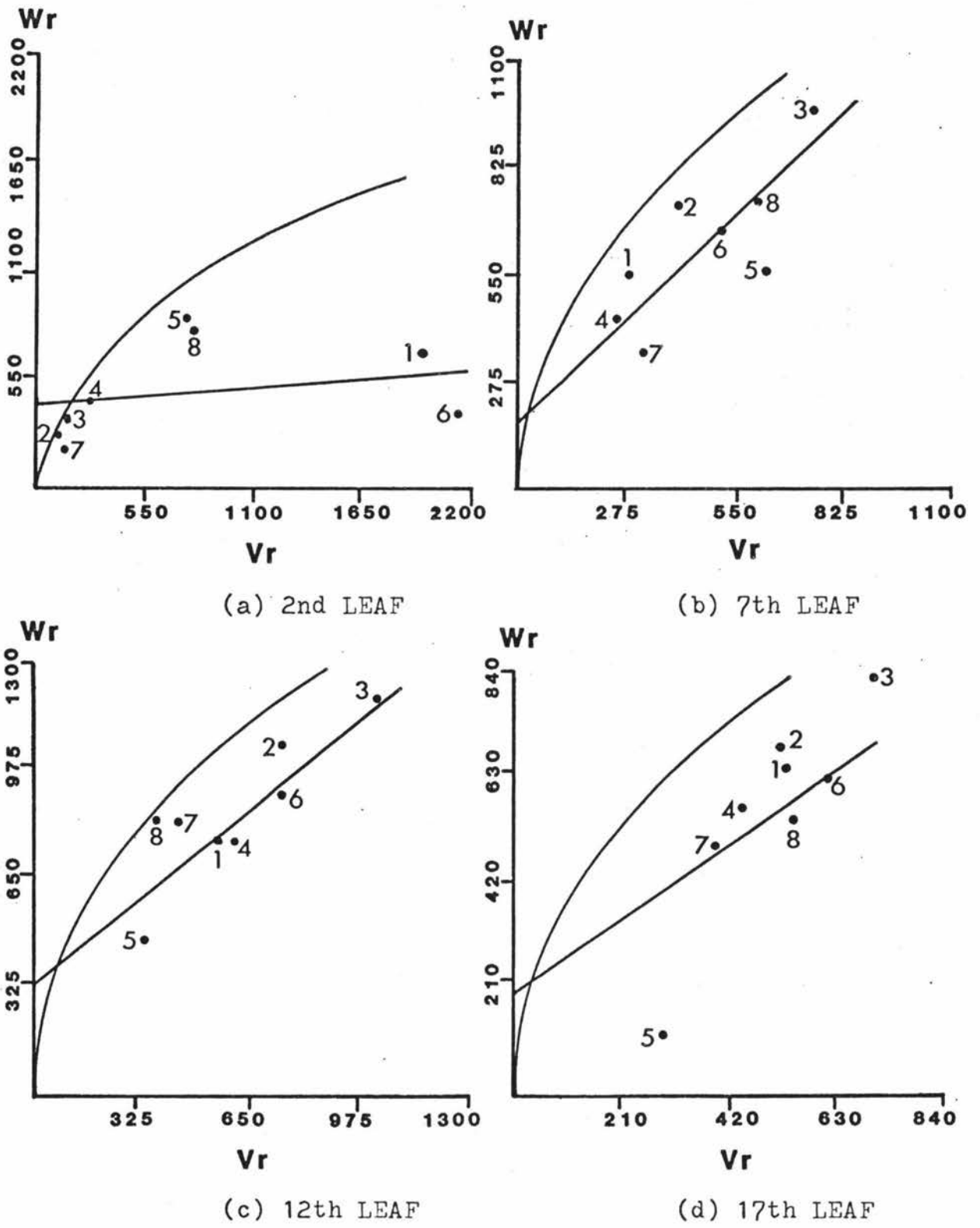


FIGURE 4.6 (W_r , V_r) GRAPHS FOR PETIOLE LENGTH

TABLE 4.9.1 WING WIDTH (ORIGINAL DATA)

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r , (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

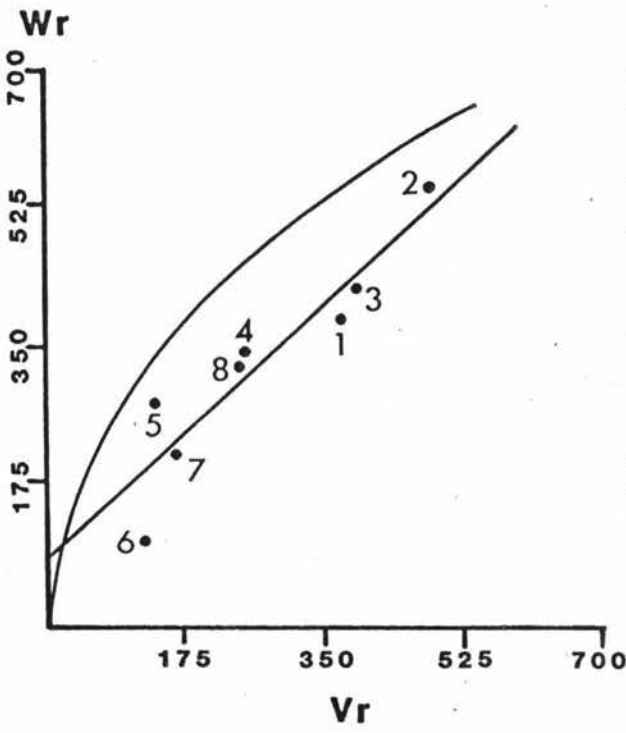
ANALYSIS		2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :		$\times 10^4$	$\times 10^4$	$\times 10^4$	$\times 10^4$
($W_r + V_r$):	df				
Array Differences	7	20.51**	25.04***	99.79***	28.32NS
Error	14	4.17	43.46	15.17	10.53
($W_r - V_r$)					
Array Differences	7	0.71NS	1.14NS	1.64N	1.11NS
Error	14	0.28	0.44	2.56	0.64
(B) (W_r , V_r) REGRESSION STATISTICS:					
W_r Intercept ($\hat{b}_0$)		90.0	135.0	219.0	102.0
Regression Coefficient ($\hat{b}_1$)		0.92	1.08	0.76	0.86
Std. Error Of $\hat{b}_1$		0.151	0.117	0.072	0.101
t - test ($\hat{b}_1 = 0$)		6.12***	9.20***	10.52***	8.53***
t - test ($\hat{b}_1 = 1$)		0.51 NS	0.46NS	3.37**	1.34NS
Coefficient of determination (R^2)		0.63	0.79	0.83	0.77
(C) (($W_r + V_r$), $\bar{P}$) CORRELATION:					
Correlation Coefficient ($\hat{r}$)		0.80****	0.68****	0.78****	0.59****
(D) GENETICAL COMPONENTS:					
$\hat{D}$		713.70	1155.76	1136.96	853.89
$\hat{H}_1$		81.98	321.59	224.21	233.43
$\hat{H}_2$		93.37	221.73	264.50	171.73
$\hat{F}$		143.90	603.25	284.99	214.10
$\hat{E}$		100.52	60.21	118.48	112.19
$\sqrt{(H_1/D)}$		0.339	0.528	0.444	0.523
$H_1/4H_2 (= \bar{UV})$		0.285	0.172	0.295	0.184
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$		0.798	0.888	0.665	0.466
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ $= K_D/K_R$		1.85	2.96	1.79	1.63

was especially so for the upper leaves (2nd and 7th leaves). This was because the dominance genetic variance ($\hat{H}_1$ and $\hat{H}_2$) were found to be smaller in the upper leaves. Both the dominance and additive genetic variances were higher in the middle leaves as compared to other leaf positions. Partial dominance was observed for all the leaf positions since $\sqrt{\hat{H}_1/\hat{D}}$ were less than unity. The partial dominance were found to be consistent across the loci for the 2nd and 7th leaves. The frequencies of positive and negative alleles were unequal as shown by the $\overline{UV}$ values for all the leaf positions. Similar results were observed from the K_D/K_R ratio and $\hat{F}$ values. More dominant alleles were present for all the leaf positions.

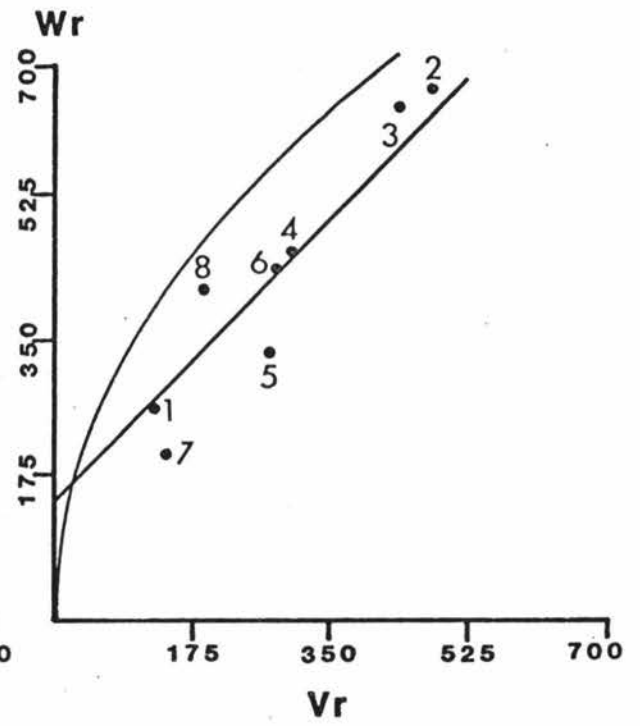
Figure 4.7.1 shows the (W_r , V_r) graphs. The R^2 obtained were generally high. The parental lines were well distributed along the regression lines. Parents 4, 5, 6, 7 and 8 which were nearer to the origin showed that more dominant alleles were present. On the other hand more recessive alleles were present in parents 1, 2 and 3.

The $((W_r + V_r), \bar{P})$ correlation coefficients were highly significant ($p=0.001$) and positive for all the leaf positions. Thus there was a strong indication that narrower wing width were due to the dominant genes.

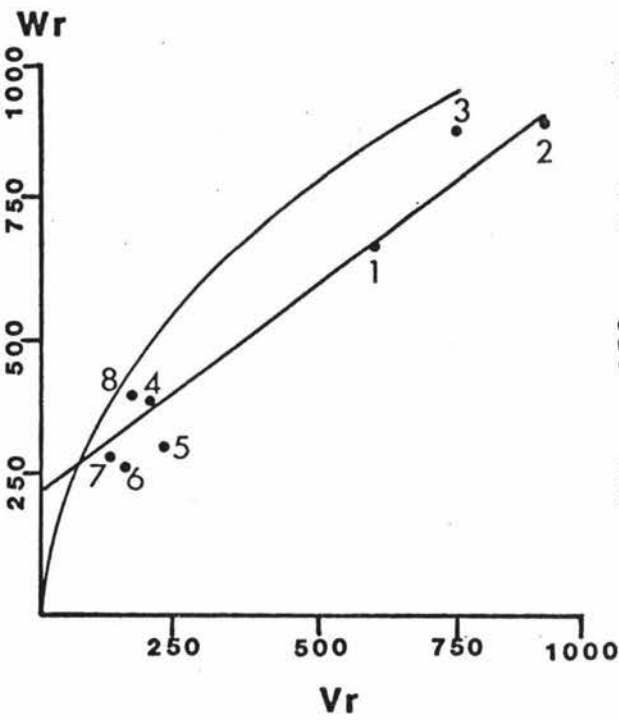
The statistics for reanalysed data (12th leaf) are shown in Table 4.9.2. By excluding parent 1, the regression coefficient ($\hat{b}_1$) was found to be larger than that of the original data. This was also shown by the



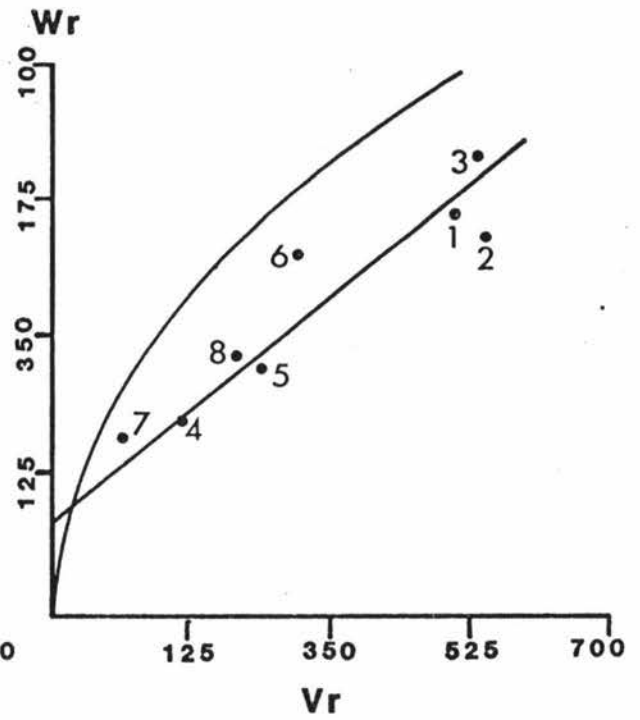
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



(d) 17th LEAF

FIGURE 4.7.1 (W_r , V_r) GRAPHS FOR WING WIDTH
(ORIGINAL DATA)

TABLE 4.9.2 WING WIDTH (REANALYSED DATA)

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r and V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENT AND (d) GENETICAL COMPONENTS ESTIMATES

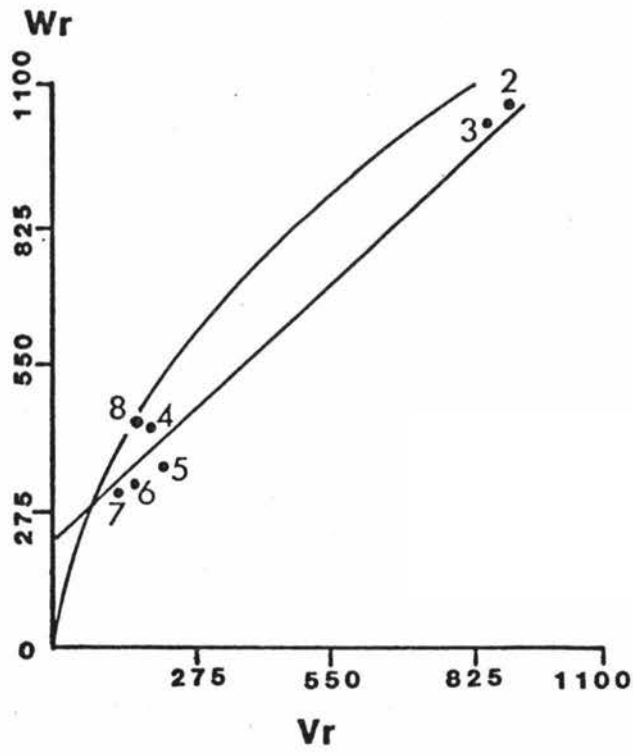
ANALYSIS	12th LEAF (PARENT 1 DELETED)
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :	$\times 10^4$
($W_r + V_r$):	df
Array Differences	6
Error	12
($W_r - V_r$):	
Array Differences	6
Error	12
(B) (W_r , V_r) REGRESSION STATISTICS:	
W_r Intercept ($\hat{b}_0$)	205.48
Regression Coefficient ($\hat{b}_1$)	0.956
Std. Error Of $\hat{b}_1$	0.073
t - test ($\hat{b}_1 = 0$)	13.06***
t - test ($\hat{b}_1 = 1$)	0.602NS
Coefficient of determination (R^2)	
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:	
Correlation Coefficient ($\hat{r}$)	0.930****
(D) GENETICAL COMPONENTS:	
$\hat{D}$	1363.48
$\hat{H}_1$	318.01
$\hat{H}_2$	314.65
$\hat{F}$	510.37
$\hat{E}$	84.71
$\sqrt{(H_1/D)}$	0.48
$H_1/4H_2 (=UV)$	0.25
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$	3.77
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$	
$= K_D/K_R$	2.27

(Wr, Vr) graph (Figure 4.7.2). The parental points were well distributed along the regression line. The distribution of the parental lines along the regression line were found to be similar to that of the original data. Generally the variance component estimates were larger than that of the original data. The interpretations based on the ratio of genetical components and the direction of dominance were also similar.

4.2.8 Wing area

Table 4.10 shows the diallel statistics for wing area.

Diallel analysis was not carried out for 2nd leaf since analysis of variance indicated that there was no significant genotypic differences. The (Wr + Vr) analysis was significant only for the 17th leaf. Thus non-additive genetic variance was found to be of little importance for this character. The (Wr - Vr) analyses were not significant for all the leaf positions. Except for the 17th leaf, test of deviation of $\hat{b}_1$ from unity was significant for all other leaf positions. This appeared to indicate the presence of inter-locus interaction. However a poor R^2 (approximately 0.23) suggested that little faith could be given to this test. Thus an overall view suggested that there was little evidence in favour on inter-locus interaction. The error variance estimates ($\hat{E}$) were relatively high for all the leaf positions. This indicated that the variance of genetical components were trivial for this character. This was supported by the presence of little dominance from (Wr + Vr) analyses of variance. The additive genetic variance



12th LEAF (PARENT 1 DELETED)

FIGURE 4.7.2 (W_r , V_r) GRAPH FOR WING WIDTH
(REANALYSED DATA)

TABLE 4.10 WING AREA

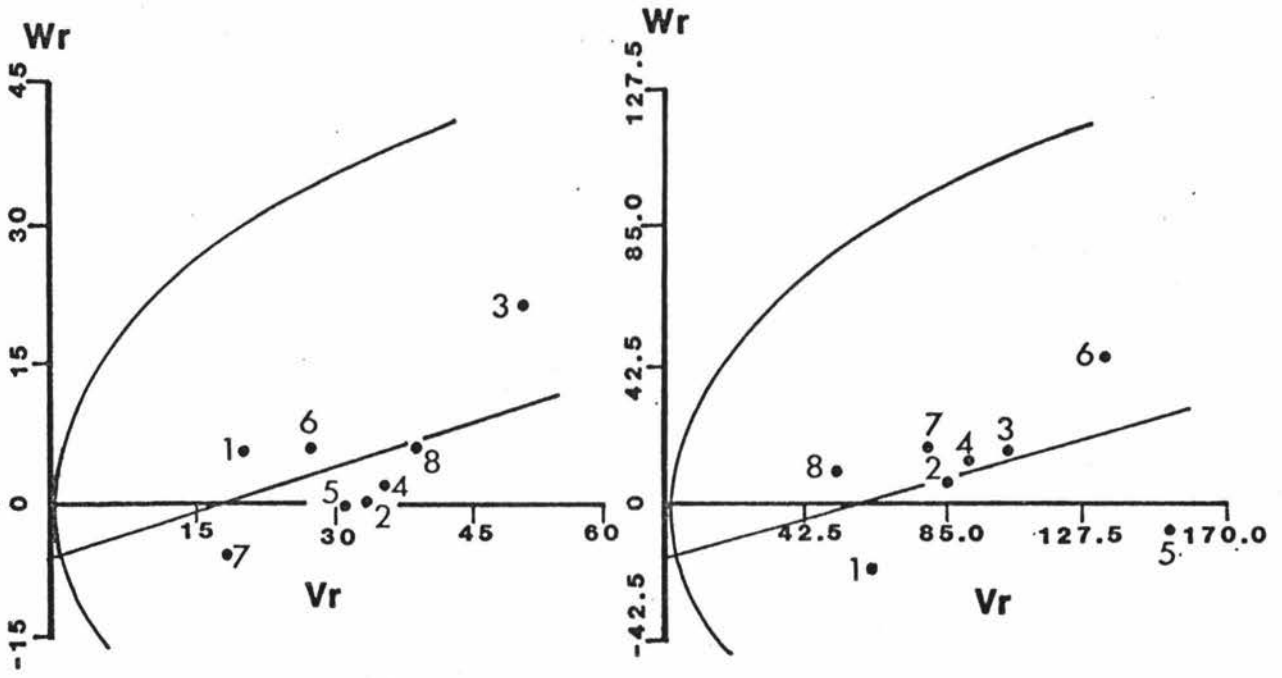
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS		7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :				
($W_r + V_r$):	df			
Array Differences	7	5681NS	20046NS	36663*
Error	14	4564	20751	11302
($W_r - V_r$)				
Array Differences	7	3519 NS	7799NS	7878NS
Error	4	1654	6598	4949
(B) (W_r , V_r) REGRESSION STATISTICS:				
W_r Intercept ($\hat{b}_0$)		19.66	1.93	33.10
Regression Coefficient ($\hat{b}_1$)		0.32	0.38	0.63
Std. Error Of ($\hat{b}_1$)		0.131	0.145	0.227
t - test ($\hat{b} = 0$)		2.40*	2.59*	2.77*
t - test ($\hat{b} = 1$)		5.21***	4.29***	1.60 NS
Coefficient of determination (R^2)		0.21	0.23	0.26
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:				
Correlation Coefficient ($\hat{r}$)		0.20NS	0.54***	0.74***
(D) GENETICAL COMPONENTS:				
$\hat{D}$		41.13	126.63	144.57
$\hat{H}_1$		3.93	151.16	141.16
$\hat{H}_2$		112.79	149.78	87.67
$\hat{F}$		74.38	70.83	164.31
$\hat{E}$		67.72	96.38	89.97
$\sqrt{(H_1/D)}$		1.258	1.871	0.988
$H_1/4H_2 (= \bar{U})$		0.196	0.248	0.155
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$		1.039	2.686	0.934
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ = K_D/K_R		2.871	1.688	3.707

estimates were higher in the bottom leaves than the top leaves. However, the dominance genetic variance estimates were higher in the middle leaves than other leaf positions. The H_1/D indicated that over dominance was present for the 7th and 12th leaves. Complete dominance was probably present for 17th leaf since the $\sqrt{H_1/D}$ values were approximately equal to 1. From the $\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$, the observed dominance was consistently distributed across all the loci only for the 7th and 17th leaves. The $\overline{UV}$ values showed that the proportions of positive and negative alleles were equally distributed only for the 12th leaf. The K_D/K_R ratio which was close to unity for the 12th leaf was consistent with the earlier statement that the positive and negative alleles were present in equal proportions. These ratios together with the $\hat{F}$ values indicated that more dominant alleles were present in other leaf positions.

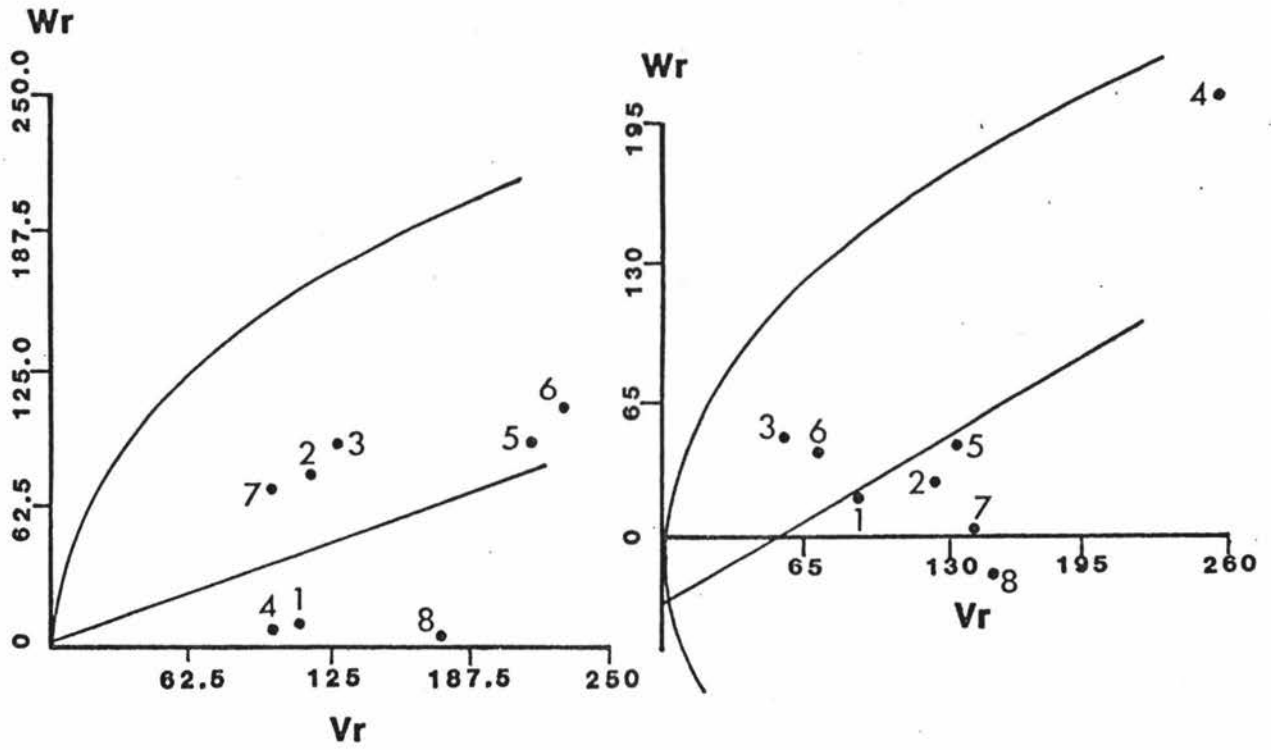
The (W_r, V_r) graphs are shown in Figure 4.8. The parental points tended to cluster together. This was as expected since very little dominance was observed for this character. Their distributions were not consistent for all the leaf positions. However, an overall view across all the leaf positions indicated that parents 7 and 1 contained most dominant alleles. Parents 6 and 5 on the otherhand contained most recessive alleles.

The $((W_r + V_r), \bar{P})$ correlation coefficients were highly significant for the 12th and 17th leaves but not for the 7th leaf. It appeared that ambidirectional dominance was present for the 7th leaf. However an



(a) 2nd LEAF

(b) 7th LEAF



(c) 12th LEAF

(d) 17th LEAF

FIGURE 4.8 (W_r , V_r) GRAPHS FOR WING AREA

overall view suggested that smaller wing area was due to the dominant genes.

4.2.9 Auricle area

The diallel statistics for both the 8 x 8 original and 7 x 7 reanalysed data are presented in Tables 4.11.1 and 4.11.2 respectively.

The $(W_r + V_r)$ estimates were homogeneous over arrays for the 7th, 12th and 17th leaves. This generally indicated that dominance was of little importance for this character. The $(W_r - V_r)$ estimates were significant for 2nd, 12th and 17th leaves. Except for the 2nd leaf, test of deviations of $\hat{b}_1$ from unity were also found to be significant. Thus the two tests of additive-dominance model contradicted with each other for the 2nd and 7th leaves. However there was a general indication that inter-locus interaction was present for this character.

For all the leaf positions, the estimates of additive genetic variance ($\hat{D}$) were much greater than the dominance genetic variance ($\hat{H}_1$ and $\hat{H}_2$). This was especially so for the bottom leaves. This was mainly due to the very little dominance genetic variance observed for the bottom leaves as shown by the $(W_r + V_r)$ analyses of variance. Both the additive and dominance genetic variances were higher for the middle as compared to the top or bottom leaves. The $\sqrt{\hat{H}_1/\hat{D}}$ indicated that the dominant alleles were consistently distributed across all the loci only for the 2nd leaf. The $\overline{UV}$ values which were approximately 0.25 for the 7th and 17th leaves indicated that the positive and negative alleles were present approximately in equal

TABLE 4.11.1 AURICLE AREA (ORIGINAL DATA)

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS		2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :					
($W_r + V_r$):	df				
Array Differences	7	4581**	5229NS	2317NS	506.4NS
Error	14	987.5	7418	1155	481.6
($W_r - V_r$)					
Array Differences	7	173.1*	3004NS	520.7*	193.10**
Error	14	53.75	1620	161.7	43.31
(B) (W_r , V_r) REGRESSION STATISTICS:					
W_r Intercept ($\hat{b}_0$)		0.47	60.13	42.24	25.11
Regression Coefficient ($\hat{b}_1$)		0.95	0.41	0.42	0.41
Std. Error of $\hat{b}_1$		0.082	0.134	0.113	0.17
t - test ($\hat{b}_1 = 0$)		11.57***	3.07***	3.74***	2.39*
t - test ($\hat{b}_1 = 1$)		0.65NS	4.38***	5.12***	3.39**
Coefficient of determination (R^2)		0.86	0.30	0.39	0.21
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:					
Correlation Coefficient ($\hat{r}$)		0.87****	0.22 NS	0.15 NS	0.32 NS
(D) GENETICAL COMPONENTS					
$\hat{D}$		59.511	191.590	113.351	73.130
$\hat{H}_1$		30.735	68.973	30.237	11.251
$\hat{H}_2$		22.423	72.915	17.526	8.889
$\hat{F}$		45.021	8.279	-33.821	-1.780
$\hat{E}$		10.045	26.561	13.989	10.412
$\sqrt{(H_1/D)}$		0.719	0.600	0.517	0.392
$H_1/4H_2 (=UV)$		0.182	0.264	0.145	0.198
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$		1.012	0.151	-0.446	-0.068
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ = K_D/K_R		3.223	1.075	0.552	0.939

proportions. The positive and negative alleles were present in unequal proportions for other leaf positions. This was supported by K_D/K_R ratio and $\hat{F}$ values. The dominant and recessive alleles were present in equal proportions for the 7th and 17th leaves. More dominant and recessive genes were present in the 2nd and 12th leaves respectively.

The (W_r, V_r) graphs are shown in Figure 4.9.1. For all the leaf positions, parents 5 and 8 have the most dominant alleles. Even though there were variations between the leaf positions, generally parent 2 was the most recessive for this character.

The $((W_r + V_r), \bar{P})$ correlation coefficients were positive for all the leaf positions. The estimates was significant only for the 2nd leaf. Generally therefore, the smaller auricle area was dominant to bigger auricle area.

By excluding parent 7 (2nd leaf), the $(W_r - V_r)$ was found to be homogeneous. $\hat{b}_1$ which was slightly larger than the original data was not significantly different from unity (Table 4.11.2). This suggested that parent 7 was responsible for the failure of the original data to satisfy the additive-dominance model. As shown by the (W_r, V_r) graph (Figure 4.9.2), the parental points along the regression line were similar to that of the original data. Estimates of the genetical components were slightly higher than that of the original data. However, the interpretations based on the ratios of genetical components remained the same.

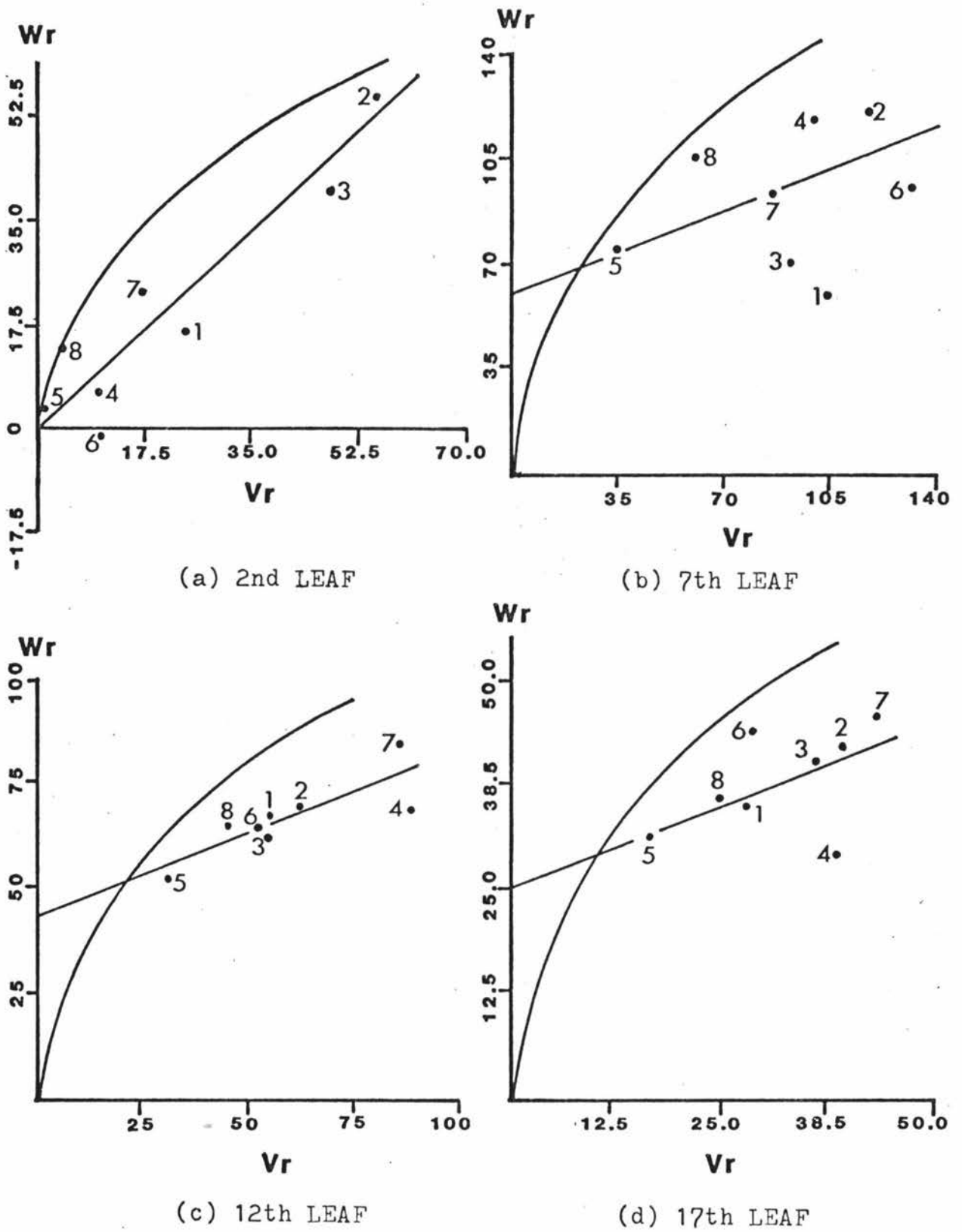
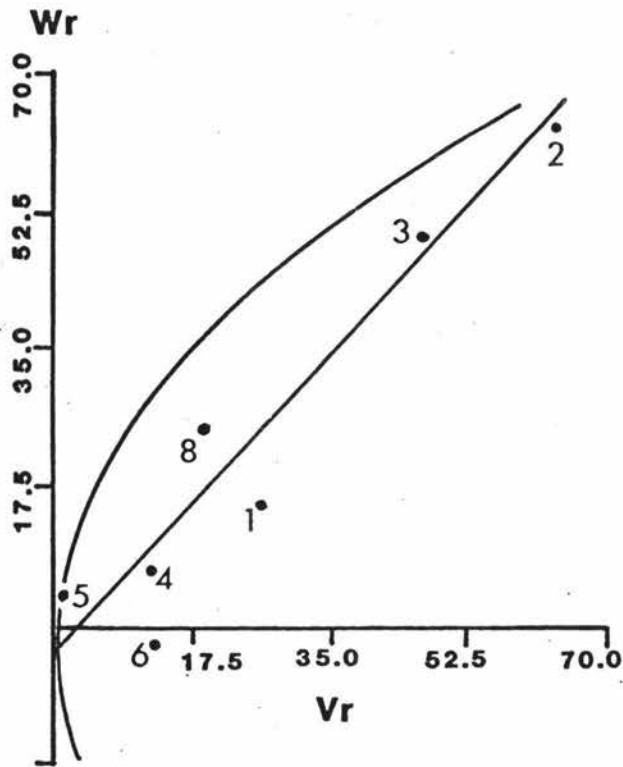


FIGURE 4.9.1 (W_r , V_r) GRAPHS FOR AURICLE AREA
(ORIGINAL DATA)

TABLE 4.11.2 AURICLE AREA (REANALYSED DATA)

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) (($W_r + V_r$), $\bar{P}$) CORRELATION
 COEFFICIENT AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS	2nd LEAF (parent 7 deleted)
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :	
($W_r + V_r$):	df
Array Differences	6 6779**
Error	12 1208
($W_r - V_r$):	
Array Differences	6 226.37 NS
Error	12 90.67
(B) (W_r , V_r) REGRESSION STATISTICS:	
W_r Intercept ($\hat{b}_0$)	-3.328
Regression Coefficient ($\hat{b}_1$)	1.054
Std. Error Of $\hat{b}_1$	0.106
t - test ($\hat{b}_1 = 0$)	9.94***
t - test ($\hat{b}_1 = 1$)	0.509 NS
Coefficient of determination (R^2)	0.853
(C) (($W_r + V_r$), $\bar{P}$) CORRELATION:	
Correlation Coefficient ($\hat{r}$)	0.949****
(D) GENETICAL COMPONENTS:	
$\hat{D}$	67.16
$\hat{H}_1$	41.55
$\hat{H}_2$	29.47
$\hat{F}$	52.31
$\hat{E}$	9.51
$\sqrt{(H_1/D)}$	0.79
$H_1/4H_2 (= \bar{UV})$	0.35
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$	0.92
$(\sqrt{(4D H_1)} + F)/\sqrt{(4D H_1) - F}$	
$= K_D/K_R$	2.96



2nd LEAF (PARENT 7 DELETED)

FIGURE 4.9.2(W_r , V_r) GRAPH FOR AURICLE AREA
(REANALYSED DATA)

4.2.10 Vein angle

Table 4.12.1 shows the diallel statistics for vein angle.

There was a strong evidence of dominance present since the analyses of $(W_r + V_r)$ were highly significant for all the leaf positions. Both the analyses of $(W_r - V_r)$ and deviations of $\hat{b}_1$ from unity were not significant except for the 2nd leaf. An overall view therefore suggested that inter-locus interaction was not important for this character. However, there was a possibility that inter-locus interaction was present only for the 2nd leaf.

The additive genetic variance estimates ($\hat{D}$) were greater than the dominance genetic variance ($\hat{H}_1$ and $\hat{H}_2$) for all the leaf positions. This was especially so for the middle leaves. Additive genetic variance were generally higher for the bottom leaves as compared to other leaf positions. Dominance genetic variance were higher for the upper leaves. Partial dominance was observed for all leaf positions, although the $\sqrt{\hat{H}_1/\hat{D}}$ value did approach unity (complete dominance) for the 2nd leaf. Dominance was consistent across the loci only for the 2nd leaf. Proportions of positive and negative alleles, as shown by the $\overline{UV}$ values, were found to be approximately equal for all the leaf positions. Both the K_D/K_R and $\hat{F}$ values indicated that approximately equal proportion of dominant and recessive alleles were present for the 12th and 17th leaves. Dominant alleles were found to be slightly greater for the 2nd and 7th leaves.

TABLE 4.12.1 VEIN ANGLE (ORIGINAL DATA)

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS	2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r:				
($W_r + V_r$):	df			
Array Differences	7 30217***	28886***	36212***	9840**
Error	14 1696	1189	4108	2285
($W_r - V_r$):				
Array Differences	7 892.5**	315 NS	615.1 NS	235.9 NS
Error	14 195.0	214	243.9	92.8
(B) (W_r, V_r) REGRESSION STATISTICS:				
W_r Intercept ($\hat{b}_0$)	13.19	19.41	49.46	46.54
Regression Coefficient ($\hat{b}_1$)	0.73	1.12	0.90	0.83
Std. Error Of $\hat{b}_1$	0.057	0.068	0.061	0.093
t - test ($\hat{b}_1 = 0$)	12.88***	16.52***	14.84***	8.94***
t - test ($\hat{b}_1 = 1$)	4.66***	1.74NS	1.64NS	1.83NS
Coefficient of determination (R^2)	0.88	0.93	0.91	0.98
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:				
Correlation Coefficient ($\hat{r}$)	0.85****	0.93****	0.81****	0.51***
(D) GENETICAL COMPONENTS:				
$\hat{D}$	127.941	218.301	270.459	225.390
$\hat{H}_1$	85.411	56.222	46.423	58.692
$\hat{H}_2$	75.384	53.578	52.705	50.157
$\hat{F}$	55.925	83.381	4.648	3.283
$\hat{E}$	12.971	15.578	18.540	10.068
$\sqrt{(H_1/D)}$	0.817	0.508	0.414	0.510
$H_1/4H_2 (= \bar{UV})$	0.221	0.238	0.284	0.214
$\frac{1}{2}F/\sqrt{D} (H_1 - H_2)$	0.781	1.736	0.056	0.037
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ = K_D/K_R	1.730	2.207	1.042	1.029

Figure 4.10.1 shows the (Wr, Vr) regression graphs. The (Wr, Vr) points were found to be well distributed along the regression lines, together with high R^2 for all the leaf positions. Thus there was a clear indication that parents 1, 2 and 3 had a greater proportion of recessive alleles for this character. The highest proportion of dominant alleles were present in parents 5 and 6.

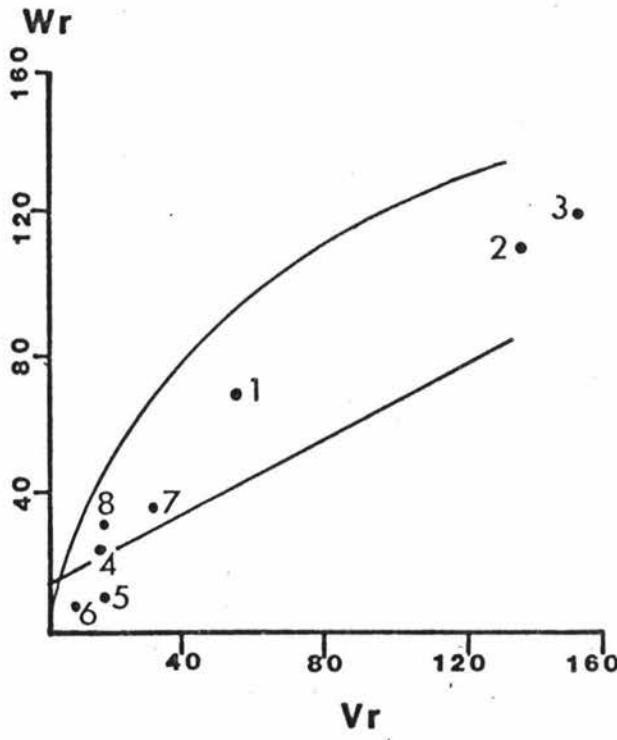
The ((Wr + Vr), $\bar{P}$) correlation coefficients were positive and highly significant for all the leaf positions. This strongly suggested that dominance was responsible for smaller vein angle.

The (Wr - Vr) analysis, together with the deviation of $\hat{b}_1$ were not significant for the reanalysed data (2nd leaf) (Table 4.12.2). This is also shown by the well distributed parental points along the regression line (Figure 4.10.2). The positions of these parental lines were similar to that of the original data. Estimates of genetical components were slightly smaller than that of the original data. However the ratios of the genetical components remained the same.

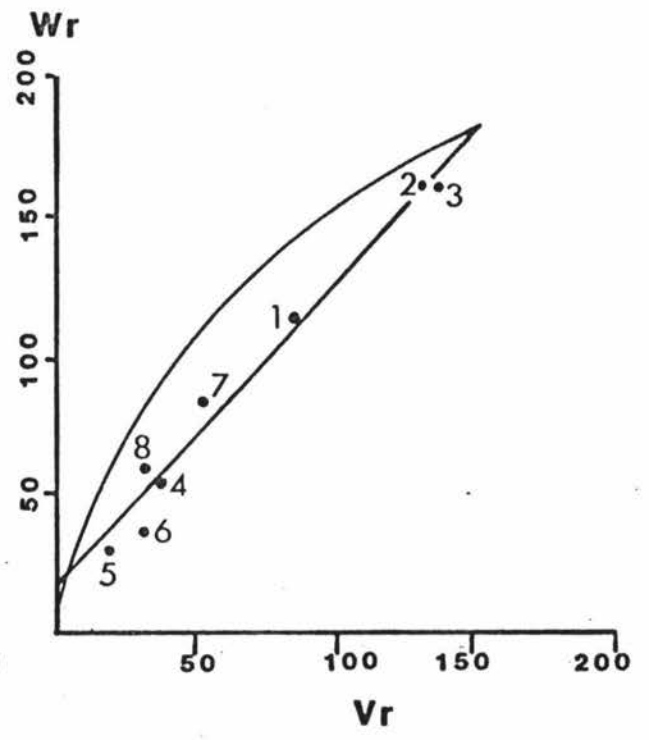
4.2.11 Leaf dry weight

The diallel statistics for leaf dry weight are presented in Table 4.13.

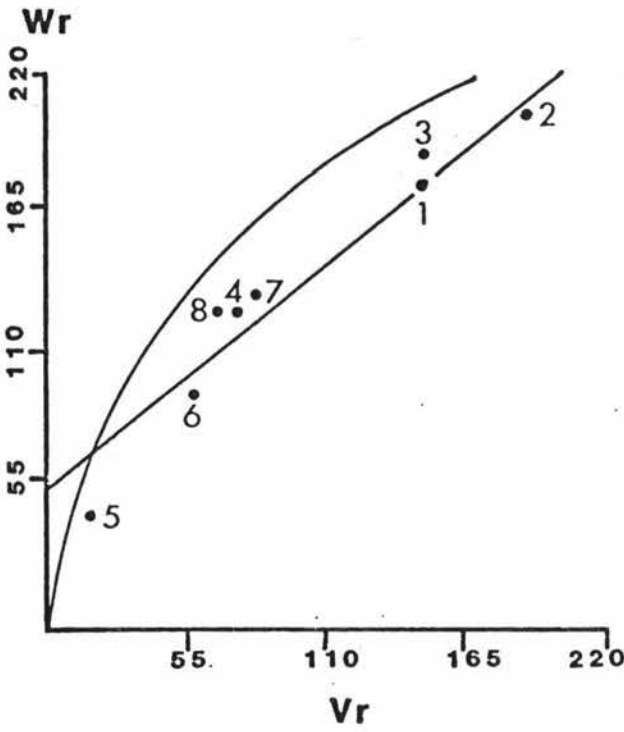
The analysis (Wr + Vr) showed that dominance was present only for the 2nd leaf. The analyses of (Wr - Vr) were not significant for the 7th and 17th leaves, but significant (at $p = 0.05$) for 2nd and 12th leaves. Deviations of $\hat{b}_1$ from unity were significant for all



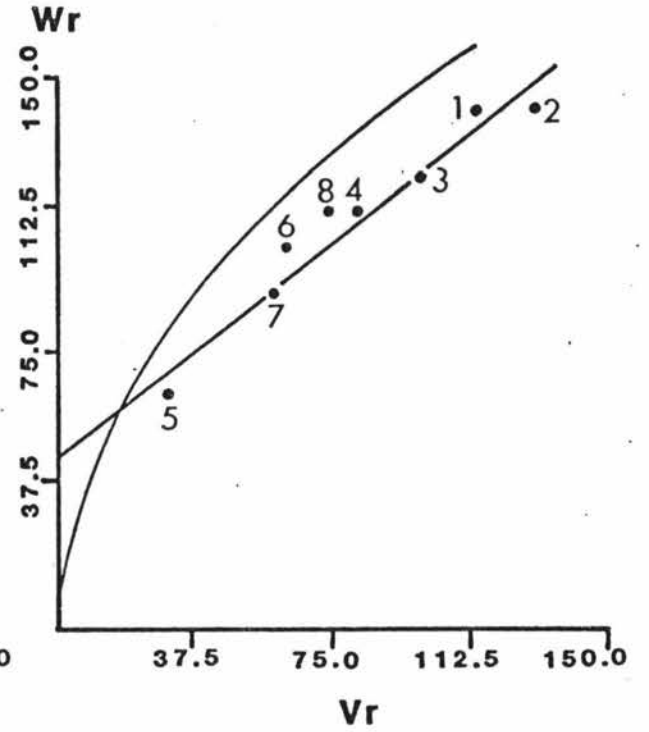
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



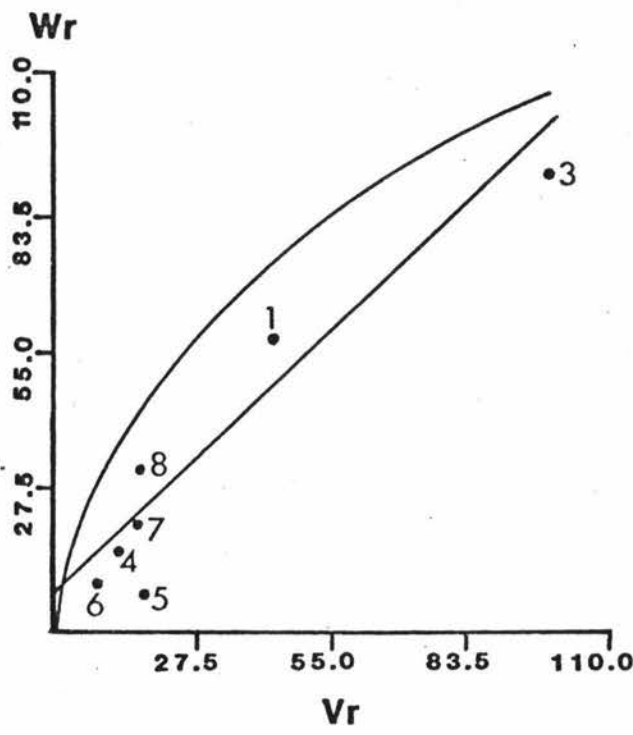
(d) 17th LEAF

FIGURE 4.10.1 (W_r , V_r) GRAPHS FOR VEIN ANGLE
(ORIGINAL DATA)

TABLE 4. 12. 2 VEIN ANGLE (REANALYSED DATA)

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS	2nd LEAF (parent 2 deleted)
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :	
($W_r + V_r$):	df
Array Differences	6 11522***
Error	12 244
($W_r - V_r$)	
Array Differences	6 288.9 NS
Error	12 117.7
(B) (W_r , V_r) REGRESSION STATISTICS:	
W_r Intercept ($\hat{b}_0$)	5.031
Regression Coefficient ($\hat{b}_1$)	0.878
Std. Error Of $\hat{b}_1$	0.094
t - test ($\hat{b}_1 = 0$)	9.340***
t - test ($\hat{b}_1 = 1$)	1.298 NS
Coefficient of determination (R^2)	0.820
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION	
Correlation Coefficient ($\hat{r}$)	0.837****
(D) GENETICAL COMPONENTS:	
$\hat{D}$	108.25
$\hat{H}_1$	67.29
$\hat{H}_2$	47.36
$\hat{F}$	96.26
$\hat{E}$	10.57
$\sqrt{H_1/D}$	0.79
$H_1/4H_2 (= \overline{UV})$	0.36
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$	1.04
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ = K_D/K_R	3.58



2nd LEAF (PARENT 2 DELETED)

FIGURE 4.10.2 (W_r , V_r) GRAPH FOR VEIN ANGLE
(REANALYSED DATA)

TABLE 4.13 LEAF DRY WEIGHT

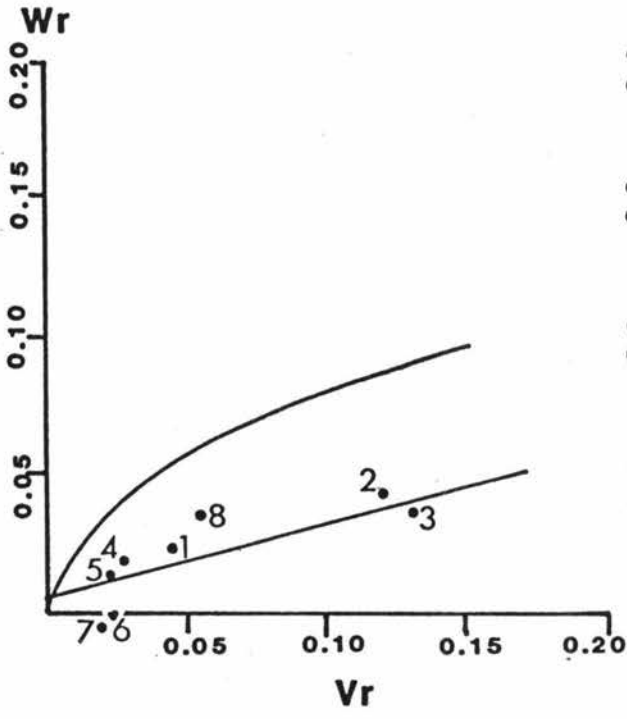
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS, AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS		2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :		$\times 10^{-2}$	$\times 10^{-2}$	$\times 10^{-2}$	$\times 10^{-2}$
($W_r + V_r$):	df				
Array Differences	7	1.06***	1.55NS	14.56NS	3.93NS
Error	14	0.14	4.39	24.01	3.73
($W_r - V_r$):					
Array Differences	7	0.32*	1.63NS	5.26*	3.07NS
Error	14	0.11	0.84	1.67	1.78
(B) (W_r , V_r) REGRESSION STATISTICS:					
W_r Intercept ($\hat{b}_1$)		0.0061	0.05	0.10	0.014
Regression Coefficient ($\hat{b}_1$)		0.25	0.52	0.60	0.20
Std. Error Of $\hat{b}_1$		0.085	0.175	0.115	0.076
t - test ($\hat{b}_1 = 0$)		2.95**	2.94**	5.26***	2.67*
t - test ($\hat{b}_1 = 1$)		8.76***	2.76*	3.45**	10.43***
Coefficient of determination (R^2)		0.28	0.28	0.56	0.24
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION:					
Correlation Coefficient ($\hat{r}$)		0.60****	0.05NS	0.37*	0.39*
(D) GENETICAL COMPONENTS					
$\hat{D}$		0.033	0.269	0.552	0.058
$\hat{H}_1$		0.069	-0.059	0.006	0.144
$\hat{H}_2$		0.052	-0.060	0.074	0.157
$\hat{F}$		-0.0005	-0.033	-0.061	-0.037
$\hat{E}$		0.031	0.165	0.203	0.150
$\sqrt{(H_1/D)}$		1.450	0.471	0.099	1.579
$H_1/4H_2 (=UV)$		0.189	0.239	-3.389	0.272
$\frac{1}{2}F/\sqrt{D(H_1 - H_2)}$		-0.011	-0.611	-0.146	-0.674
$(\sqrt{(4DH_1)} + F)/(\sqrt{(4DH_1)} - F)$ = K_D/K_R		0.990	0.768	0.285	0.665

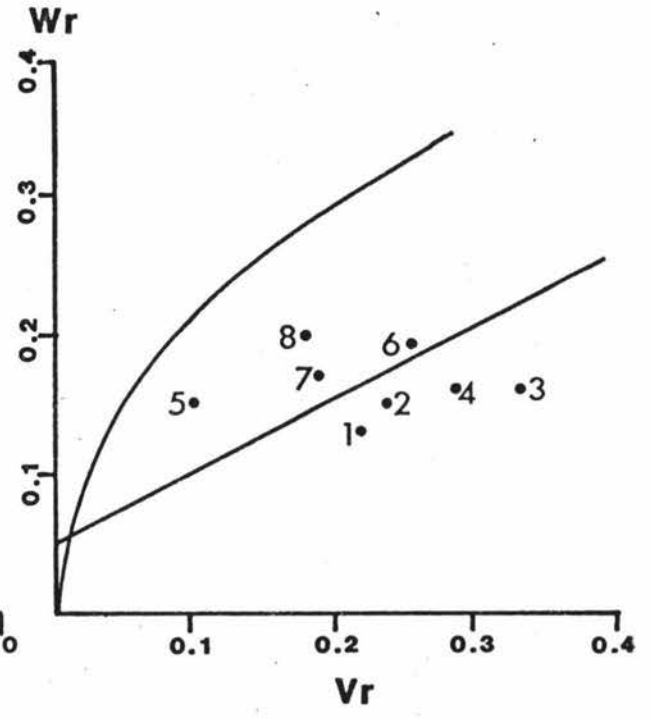
the leaf positions. However this test was equivocal since R^2 obtained from (Wr, Vr) regressions were relatively low (0.24 to 0.56). An overall view therefore suggested that interlocus interaction was probably of little importance.

Except for the 2nd leaf, additive genetic variance estimates ($\hat{D}$) were greater than the dominance genetic variances ($\hat{H}_1$ and $\hat{H}_2$) for other leaf positions. For the 2nd leaf dominance genetic variances were approximately two times greater than additive genetic variance. Consistent results were observed from (Wr + Vr) analyses of variance. Highest additive genetic variance was observed for the middle leaves. On the other hand the dominance genetic variance was highest for the bottom leaves. The $\sqrt{\hat{H}_1/\hat{D}}$ showed the presence of partial dominance for the 7th and 12th leaves. However over-dominance was present for the 2nd and 17th leaves. The $\frac{1}{2}\hat{F}/\sqrt{\hat{D}} (\hat{H}_1 - \hat{H}_2)$ ratio showed that the dominance was not consistently distributed across all loci. The proportions of positive and negative alleles were approximately equal in 2nd, 7th and 17th leaves, but not for the 12th leaf. This was consistent with the $\hat{F}$ and K_D/K_R values obtained. The number of dominant and recessive genes were present approximately in equal proportions for the 2nd, 7th and 17th leaves. More recessive genes were present for the 12th leaf.

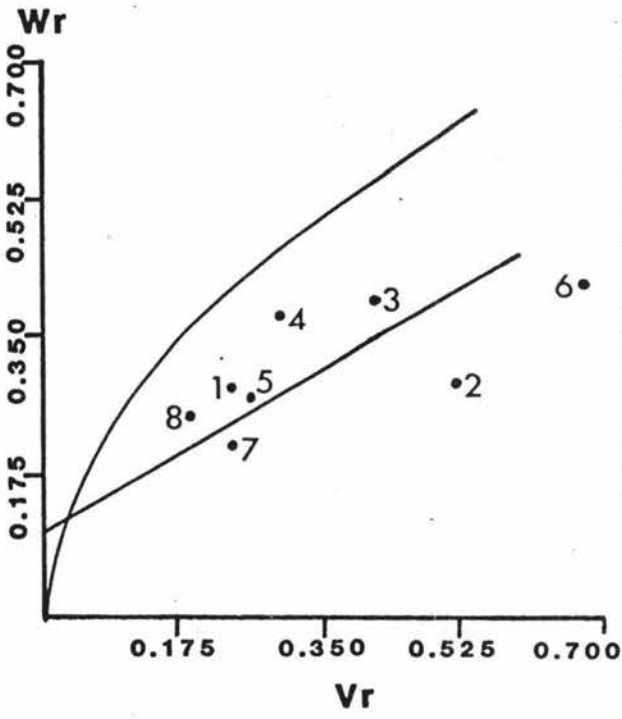
Graphical analyses (Figure 4.11) showed that parent 3 contained most recessive alleles for the 2nd and 7th leaves. For 12th and 17th leaves, most recessive



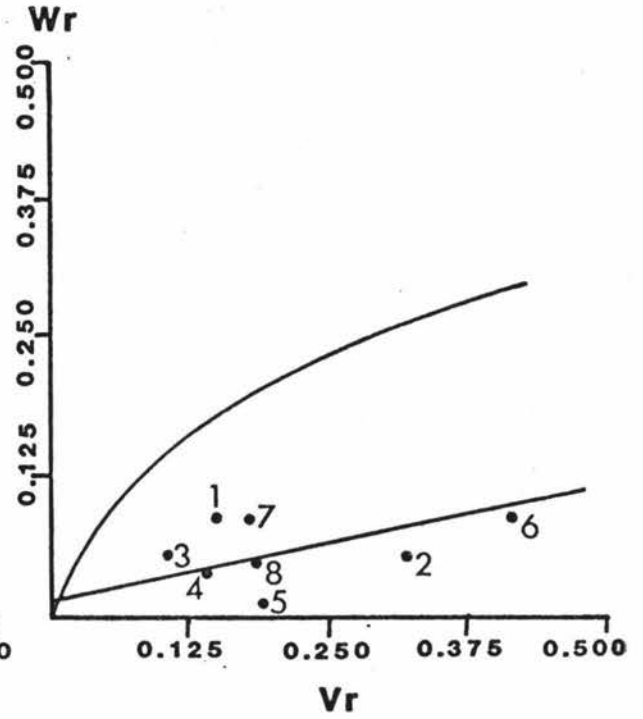
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



(d) 17th LEAF

FIGURE 4.11 (W_r , V_r) GRAPHS FOR LEAF DRY WEIGHT

alleles were present in parents 2 and 6. The parents which contained most dominant alleles were not clearly shown by the graphs. The positions of the parental points were also not consistent across the leaf positions. This was probably a result of weak dominance as observed in the other statistics as well.

The $((Wr + Vr), \bar{P})$ correlation coefficients, which were positive and significant for all the leaf positions except the 7th, indicated that dominance was responsible for the lower dry weights.

4.2.12 Leaf area

The diallel statistics for leaf area are given in Table 4.14.

Both the $(Wr + Vr)$ and $(Wr - Vr)$ analyses of variance were not significant for all the leaf positions. Deviations of $\hat{b}_1$ from unity were also not significant for the 2nd and 12th leaves. Thus there was little evidence for dominance or inter-locus interaction present.

The additive genetic variance estimates ($\hat{D}$) were generally higher than the dominance genetic variance ($\hat{H}_1$ and $\hat{H}_2$) for all the leaf positions. This was consistent with the $(Wr + Vr)$ analyses of variance. All the components of genetic variation ($\hat{D}$, $\hat{H}_1$ and $\hat{H}_2$) were found to be higher in the middle as compared to the top or bottom leaves. The $\sqrt{\hat{H}_1/\hat{D}}$ value indicated that partial dominance was observed for all the leaf positions. The distribution of dominance and recessive alleles were consistent across all the loci only for the 2nd leaf. The $\overline{UV}$ values indicated that the positive

TABLE 4.14 LEAF AREA

(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r and V_r ,
 (B) (W_r , V_r) REGRESSION STATISTICS, (C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION
 COEFFICIENTS AND (D) GENETICAL COMPONENTS ESTIMATES

ANALYSIS	2nd LEAF	7th LEAF	12th LEAF	17th LEAF
(A) MEAN SQUARES OF THE ANALYSES OF VARIANCE OF W_r AND V_r :				
($W_r + V_r$):	df			
Array Differences	7 7720 NS	51970 NS	222800NS	29200 NS
Error	14 3847	25220	108200	30190
($W_r - V_r$):				
Array Differences	7 246.4NS	6124 NS	4654 NS	2730 NS
Error	14 113.5	4730	8498	13150
(B) (W_r , V_r) REGRESSION STATISTICS:				
W_r Intercept ($\hat{b}_0$)	633	3166	6447	2500
Regression Coefficient ($\hat{b}_1$)	0.86	0.55	0.99	0.38
Std. Error Of $\hat{b}_1$	0.086	0.137	0.133	0.158
t - test ($\hat{b}_1 = 0$)	10.02***	3.98***	7.38***	2.42*
t - test ($\hat{b}_1 = 1$)	1.67 NS	3.28**	0.09NS	3.92***
Coefficient of determination (R^2)	0.82	0.42	0.71	0.21
(C) ($(W_r + V_r)$, $\bar{P}$) CORRELATION				
Correlation Coefficient ($\hat{r}$)	0.93****	0.48**	0.51***	0.14NS
(D) GENETICAL COMPONENTS				
$\hat{D}$	6277.99	28188.85	77844.94	14282.90
$\hat{H}_1$	1120.36	9466.76	7323.77	8037.31
$\hat{H}_2$	537.36	3441.19	11859.94	5402.12
$\hat{F}$	4085.61	14009.87	19985.43	-9695.82
$\hat{E}$	2789.40	9900.30	13225.00	15694.39
$\sqrt{(H_1/D)}$	0.422	0.579	0.307	0.750
$H_1/4H_2 (= \bar{UV})$	0.119	0.091	0.405	0.168
$\frac{1}{2}F/\sqrt{D (H_1 - H_2)}$	1.068	0.538	0.532	-0.790
$(\sqrt{(4D H_1)} + F) (\sqrt{(4D H_1)} - F)$ = K_D/K_R	7.706	2.502	2.439	0.377

and negative alleles were not present in equal proportions for all the leaf positions. This was supported by the K_D/K_R and $\hat{F}$ values obtained. More dominant alleles were observed for the 2nd, 7th and 12th leaves, while more recessive alleles were present in the 17th leaf.

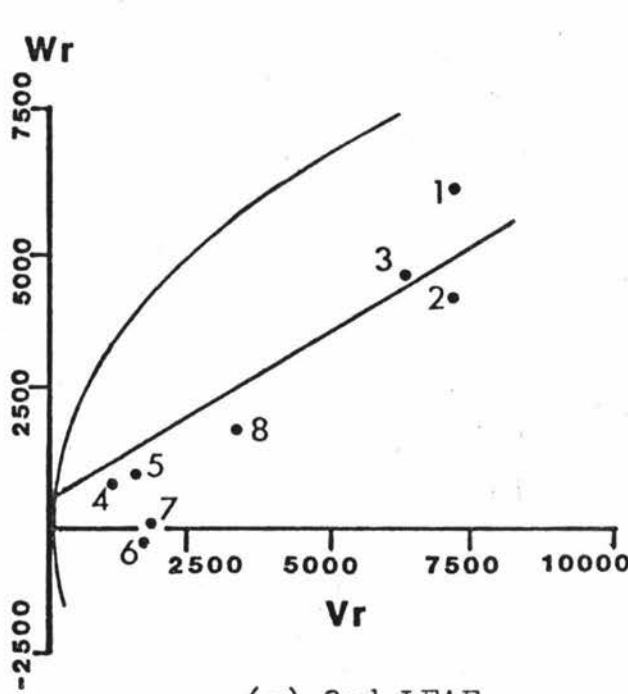
The little importance of dominance was also shown by the (Wr, Vr) graphs (Figure 4.12). The (Wr, Vr) points had no consistent pattern across all the leaf positions. However there were indications that parent 4 contained the most dominant alleles for all the leaf positions. Parent 2 appeared to contain most recessive alleles.

The ((Wr + Vr), $\bar{P}$) correlation coefficients were positive for all the leaf positions. These coefficients were significant except the 7th leaf. This indicated that dominant genes were responsible for smaller leaf area.

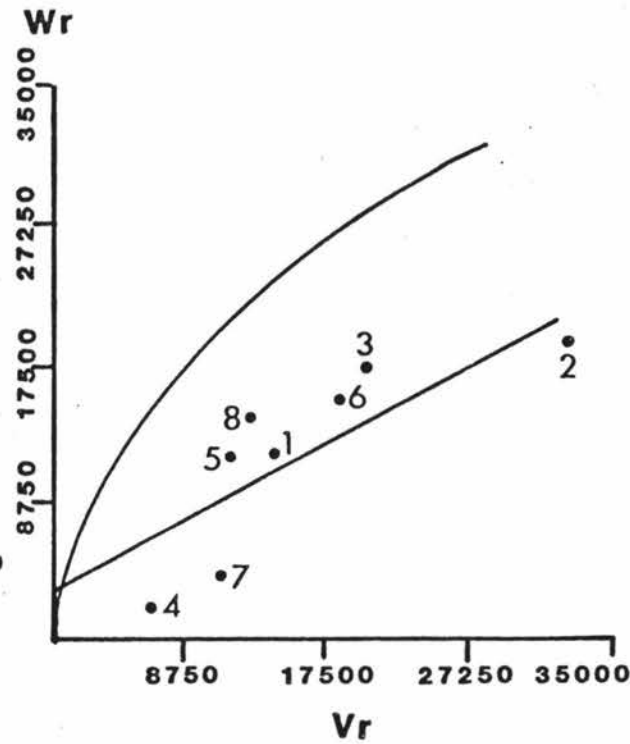
4.3 HERITABILITY ESTIMATES

Both the narrow and broadsense heritability estimates are presented in Table 4.15.

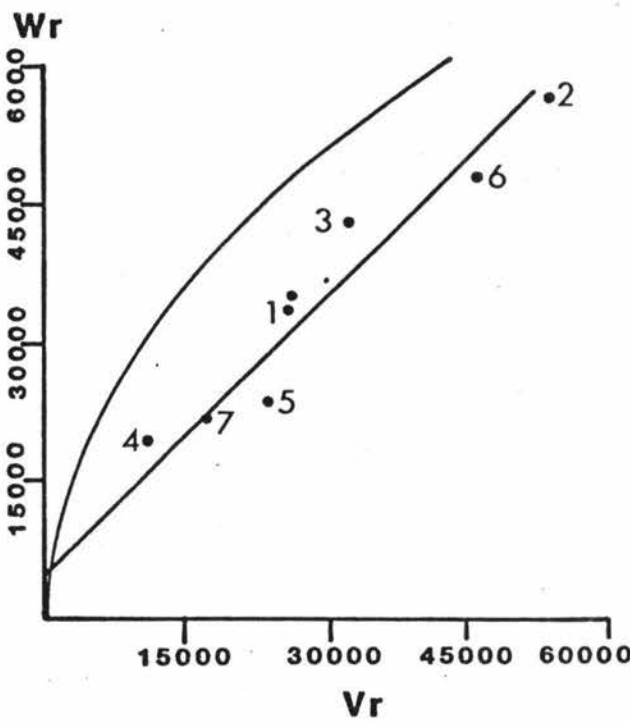
The narrowsense heritability estimates were low (approximately 20 %) to moderate (approximately 50 %) for Raper's Index I and II, differential index and wing area. The estimates were moderately high (approximately 60 - 70 %) for leaf ratio, vein angle, wing width, auricle area, petiole length and tip scores. The estimated value for both of the leaf size characters, that is leaf area and leaf dry weight, were found to be generally lower than other leaf



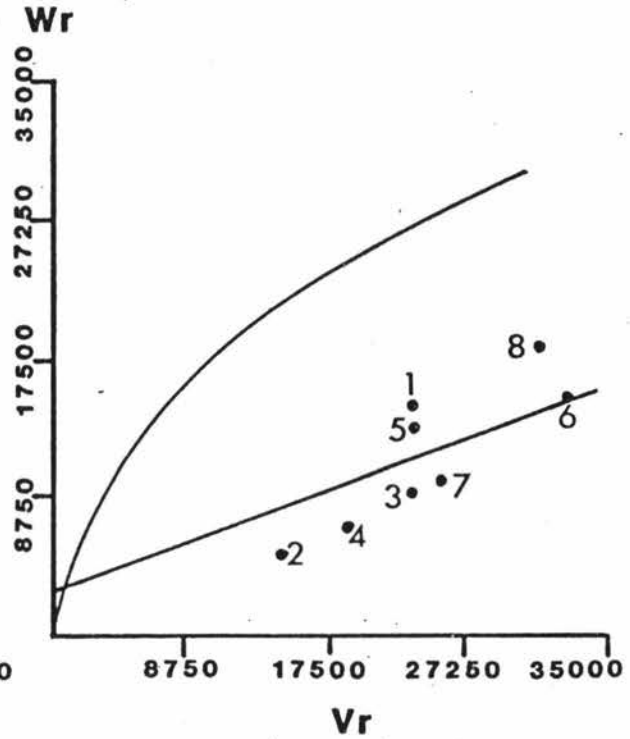
(a) 2nd LEAF



(b) 7th LEAF



(c) 12th LEAF



(d) 17th LEAF

FIGURE 4.12 (W_r , V_r) GRAPHS FOR LEAF AREA

TABLE 4.15

HERITABILITY ESTIMATES FOR BOTH 8 x 8 ORIGINAL
DATA AND REANALYSED DATA (IN BRACKETS)

CHARACTER	h^2 NARROW (%)	h^2 BROAD (%)
1. LEAF RATIO		
a) 2nd leaf	62.5	81.1
b) 7th leaf	73.2	82.8
c) 12th leaf	77.4	84.9
d) 17th leaf	64.3	75.1
2. DIFFERENTIAL INDEX		
a) 2nd leaf	48.0	61.3
b) 7th leaf	26.8	44.9
c) 12th leaf	24.6	31.8
d) 17th leaf	-6.5	12.9
3. RAPER'S INDEX I		
a) 2nd leaf	0.6	8.8
b) 7th leaf	9.5	32.4
c) 12th leaf	36.6	45.9
d) 17th leaf	11.9	26.2
4. RAPER'S INDEX II		
a) 2nd leaf	46.9	71.9
b) 7th leaf	43.8	74.0
c) 12th leaf	28.7	50.4
d) 17th leaf	33.4	73.4
5. TIP SCORE (NORMALISED)		
a) 2nd leaf	60.1	75.4
b) 7th leaf	74.8	80.9
c) 12th leaf	74.1	70.3
d) 17th leaf	60.7	68.0
6. PETIOLE LENGTH		
a) 2nd leaf	32.6	36.2
b) 7th leaf	70.4	79.7
c) 12th leaf	73.7	80.8
d) 17th leaf	64.2	68.3
7. WING WIDTH		
a) 2nd leaf	69.3	75.1
b) 7th leaf	73.8	86.4
c) 12th leaf	68.7 (72.4)	79.9 (85.7)
d) 17th leaf	69.3	77.8

TABLE 4.15 (Cont.)

CHARACTER	h^2 NARROW (%)	h^2 BROAD (%)
8. WING AREA		
a) 2nd leaf	-3.4	6.6
b) 7th leaf	-1.1	28.6
c) 12th leaf	17.6	40.7
d) 17th leaf	13.1	30.1
9. AURICLE AREA		
a) 2nd leaf	42.2 (44.4)	62.9 (68.7)
b) 7th leaf	66.7	80.3
c) 12th leaf	81.3	85.8
d) 17th leaf	75.4	79.7
10. VEIN ANGLE		
a) 2nd leaf	56.3 (41.6)	82.2 (72.5)
b) 7th leaf	70.4	84.1
c) 12th leaf	80.4	88.5
d) 17th leaf	83.6	92.7
11. LEAF DRY WEIGHT		
a) 2nd leaf	36.4	55.4
b) 7th leaf	49.9	45.1
c) 12th leaf	54.7	58.5
d) 17th leaf	17.8	34.8
12. LEAF AREA		
a) 2nd leaf	32.2	35.3
b) 7th leaf	48.4	52.6
c) 12th leaf	62.2	69.1
d) 17th leaf	43.8	48.2

characters. The values obtained ranged from 18 to 60 %.

Similar trends were observed also for the broadsense estimates. Not much difference was observed between the two types of estimates. This indicated that little non-additive genetic variance was present for most of the characters. This is consistent with the genetical variance components estimates as discussed in Section 4.2.

The heritability estimates for the reanalysed data are also shown in Table 4.15 (in brackets). The estimates obtained were higher than that of the original data for wing width (12th leaf) and auricle area (2nd leaf). However, lower estimates were obtained for vein angle (2nd leaf).

4.4 HETEROSIS

Heterosis (i.e. per centage deviation of F_1 hybrids from midparental value) are presented in Table 4.16 for all cross combinations. The estimates were made only for the characters leaf dry weight and leaf area.

Only few cases of heterosis were observed for both characters. Heterosis were often observed in hybrids involving parents with widely different phenotypic values. These were the hybrids between parents 1, 2 and 3, and the others (i.e. parents 4, 5, 6, 7 and 8).

The observed heterosis had no consistent trend across the leaf positions.

4.5 CORRELATION STUDIES

In order to study the association between the

TABLE 4.16
 HETEROSIS: PER CENTAGE DEVIATION OF F_1 HYBRIDS
 FROM MIDPARENTAL VALUES FOR LEAF AREA AND LEAF
 DRY WEIGHT

1. LEAF AREA

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
21	-22.18	-12.76	-12.2	15.33
31	-5.33	-12.46	-13.9	11.96
32	25.90	1.79	-13.9	11.11
41	-44.16	-19.01	-16.6	13.79
42	-42.05	-22.45	-17.1	13.78
43	-36.65	-10.95	-16.8	1.99
51	-30.52	-26.28	-19.4	-13.79
52	-46.36	-36.16*	-33.2**	-7.55
53	-9.76	5.14	-8.1	-1.72
54	-50.47	-14.69	3.2	-2.80
61	-25.44	-5.24	-18.9	1.24
62	-13.83	2.64	2.9	24.93*
63	-31.98	3.09	-12.4	9.96
64	-2.01	10.07	-1.3	-3.23
65	-44.97	-38.82	-40.8	-33.35*
71	-29.48	-17.74	-6.0	-8.90
72	-43.21	-21.12	-23.5*	1.19
73	-43.21	19.20	-7.4	-13.71
74	-14.45	10.03	3.6	3.06
75	-14.68	-18.21	0.9	-24.74*
76	13.83	-5.21	-12.8	-31.77*
81	-16.23	-12.50	6.2	5.01
82	-21.53	-0.81	-6.6	22.61
83	23.11	-2.30	-13.3	18.29
84	-22.27	16.82	8.1	36.57*
85	-58.21	-34.90	-15.5	-17.56
86	-46.55	-29.53	-30.8	1.65
87	10.44	20.64	20.9	13.48

TABLE 4.16 (Cont.)

2. LEAF DRY WEIGHT

GENOTYPES	2nd LEAF	7th LEAF	12th LEAF	17th LEAF
21	30.97	3.28	-4.85	13.32
31	-19.23	- 0.23	-11.84	11.32
32	98.50	9.29	-2.24	12.73
41	-25.00	-21.36	-0.25	5.45
42	18.52	5.39	25.53	14.80
43	-19.35	10.57	-2.35	15.53
51	-15.09	-14.04	-13.75	-20.53
52	18.07	-7.14	2.28	21.96
53	-20.63	-5.81	-3.03	-1.23
54	-48.65	-11.60	3.91	9.75
61	-0.90	-3.03	-0.79	-9.09
62	47.73	27.54	45.61**	51.21
63	-23.66	13.85	-11.43	22.58
64	13.92	11.33	-11.70	-13.99
65	-38.27	-10.55	-16.48	-9.19
71	-8.74	-11.27	-6.40	-18.82
72	10.00	9.69	-14.76	-5.36
73	-41.46	18.11	-5.24	-3.42
74	7.04	0.00	16.08	5.24
75	-17.81	-18.73	-1.40	-20.00
76	5.13	-3.38	2.02	-24.89
81	1.56	-4.50	-13.35	-5.06
82	35.24	13.79	-5.88	15.15
83	13.51	-7.93	-14.29	10.18
84	-12.50	4.29	12.20	37.91*
85	-57.14*	-20.83	-11.74	-12.73
86	-32.04	-14.93	-22.73	-0.84
87	15.79	10.37	1.50	4.35

N.B. Refer to Section 3.2 for the system used to code the genotypes:

- | | |
|----------------|---------------|
| 1 - TI 1372 | 5 - HFCA 250 |
| 2 - HFCA 207 | 6 - HFCA 168 |
| 3 - HFCA 220 | 7 - KUAKA 860 |
| 4 - 20728 - 92 | 8 - HFCA 241 |

characters, both the genotypic and phenotypic correlation were computed for the important pairs of characters. These coefficients are presented in Table 4.18 (phenotypic) and Table 4.17 (genotypic).

The phenotypic correlation coefficients (r_p) were highly significant for most examined pairs of characters.

Leaf ratio was found to be positively correlated with differential index, vein angle, leaf dry weight and total leaf area.

Similar results were obtained for the genotypic correlation coefficients (r_G) with respect to their trends in value and direction amongst character pairs. However the genotypic correlation coefficients were slightly higher in value than the phenotypic correlation coefficients.

TABLE 4.17
GENOTYPIC CORRELATION COEFFICIENTS (r_G) BETWEEN
SELECTED PAIRS OF CHARACTERS

CHARACTERS	2nd LEAF	7th LEAF	2th LEAF	17th LEAF
LENGTH/WIDTH AND				
-DIFFERENTIAL INDEX	-0.71****	-0.68****	-0.59****	-0.46**
-TIP SCORE	0.74****	0.89****	0.86****	0.83****
-PETIOLE LENGTH	0.64****	0.77****	0.79****	0.70****
-VEIN ANGLE	-0.61****	-0.71****	-0.81****	-0.80****
-DRY WEIGHT	-0.60****	-0.85****	-0.80****	-0.49***
-LEAF AREA	-0.63****	-0.86****	-0.84****	-0.83***
DIFFERENTIAL INDEX AND				
-TIP SCORE	-0.88****	-0.73****	-0.53****	0.34*
-PETIOLE LENGTH	-0.63****	-0.72****	-0.57****	-0.20 NS
-VEIN ANGLE	0.77****	0.69****	0.42*	0.17 NS
-DRY WEIGHT	0.45***	0.64****	0.42*	-0.11 NS
-LEAF AREA	0.44**	0.60****	0.33*	0.13 NS
TIP SCORE AND				
-PETIOLE LENGTH	0.52***	0.76****	0.82****	0.78****
-VEIN ANGLE	-0.89****	-0.86****	-0.91****	-0.83****
-DRY WEIGHT	-0.66****	-0.80****	-0.83****	-0.47***
PETIOLE LENGTH AND				
-WING WIDTH	-0.57****	-0.84****	-0.84****	-0.88****
-DRY WEIGHT	-0.28(NS)	-0.83****	-0.78****	-0.60****
VEIN ANGLE AND				
-LEAF AREA	0.72****	0.83****	0.91****	0.86****
AURICLE AREA AND				
-WING WIDTH	0.91****	0.86****	0.83****	0.82****
DRY WEIGHT AND				
-LEAF AREA	0.86****	0.85****	0.89****	0.78****

TABLE 4.18
PHENOTYPIC CORRELATION COEFFICIENTS (r_p) BETWEEN
SELECTED PAIRS OF CHARACTERS

CHARACTER	2nd LEAF	7th LEAF	12th LEAF	17th LEAF
LENGTH/WIDTH AND				
-DIFFERENTIAL INDEX	-0.65****	-0.50****	-0.48****	-0.41****
-TIP SCORE	0.68****	0.79****	0.80****	0.74****
-PETIOLE LENGTH	0.59****	0.67****	0.69****	0.61****
-VEIN ANGLE	-0.53****	-0.67****	-0.76****	-0.71****
-DRY WEIGHT	-0.50****	-0.67****	-0.71****	-0.33****
-LEAF AREA	-0.50****	-0.70****	-0.76****	-0.67****
DIFFERENTIAL INDEX AND				
-TIP SCORE	-0.76****	-0.50****	-0.41****	-0.27***
-PETIOLE LENGTH	-0.50****	-0.52****	-0.47****	-0.20*
-VEIN ANGLE	0.66****	0.54****	0.33****	0.14 NS
-DRY WEIGHT	0.32***	0.41****	0.34****	-0.13 NS
-LEAF AREA	0.30***	0.38****	0.23*	-0.01 NS
TIP SCORE AND				
-PETIOLE LENGTH	0.40****	0.69****	0.68****	0.60****
-VEIN ANGLE	-0.82****	-0.79****	-0.83****	-0.72****
-DRY WEIGHT	-0.58****	-0.67****	-0.69****	-0.23****
PETIOLE LENGTH AND				
-WING WIDTH	-0.44****	-0.76****	-0.76****	-0.77****
-DRY WEIGHT	-0.58****	-0.67****	-0.69****	-0.23****
VEIN ANGLE AND				
-LEAF AREA	0.57****	0.70****	0.82****	0.67****
AURICLE AREA AND				
-WING WIDTH	0.82****	0.81****	0.76****	0.69****
DRY WEIGHT AND				
-LEAF AREA	0.82****	0.77****	0.82****	0.69****

5. GENERAL DISCUSSION

5.1 PHENOTYPIC ANALYSIS

Except for the wing width (2nd leaf), the genotype variance component estimates were found to be significant for all characters. Their ratios to error were also consistently greater than unity. This suggested that there was a high genetic variability for the characters studied. Detailed diallel analyses such as estimation of components of genetic variance were therefore justified for these characters.

Generally it was observed that the leaves were smaller (smaller leaf area and leaf dry weight) in the top of the plant. An overall view showed that narrow leaves had more attenuated tips, more acute angles of venation, longer petioles and smaller wing widths.

The two indicators of leaf size (leaf area and leaf dry weight) indicated that these leaves were much smaller than those of commercially grown tobacco. This was probably due to the growing conditions. Also, the plants were not topped (removal of inflorescence). It has been shown that topping significantly increases the leaf dry weight and leaf area (Papenfus, 1970).

5.2 DIALLEL ANALYSIS

5.2.1 Validity of assumptions

Mather and Jinks (1971, 1977) showed that there were two tests of additive-dominance model. The presence of inter-locus interaction can be shown by the heterogeneous ($W_r - V_r$) or significant deviation of

(Wr, Vr) regression coefficient ($\hat{b}_1$) from unity.

Of all the 48 attributes (12 characters and 4 leaf positions), the analyses of (Wr - Vr) were significant only for 13 of them. Even then, except for Raper's index II (7th and 17th leaves) and vein angle (2nd leaf), they were significant only at $p = 0.05$. It is important to note that such level of significance should not be taken as unequivocal. This suggested that (Wr - Vr) were homogeneous for most characters studied. The homogeneous (Wr - Vr) indicated that inter-locus interaction were absent for these characters. Similar results were obtained from the (Wr, Vr) regression statistics. Except for Raper's index I (2nd and 12th leaves) and petiole length (2nd leaf), $\hat{b}_1$ were significant for other attributes. This generally suggested that there were straight-line sloping relationships between Wr and Vr for these attributes. The deviations of $\hat{b}_1$ from unity were generally not significant. In cases where the deviations were found to be significant, the results were equivocal since the R^2 obtained were low. This happened normally in the presence of very little dominance (homogeneous (Wr + Vr)). From these two tests it appeared that the inter-locus interaction (epistasis) was not important in the materials and characters studied. This was supported by earlier studies reported on tobacco. Matzinger et al. (1960, 1966, 1972), Matzinger (1968) and Legg and Collins (1971a, 1971b, 1975) showed that the additive X additive epistatic variance component had very little contribution to the total genetic variance.

Similar conclusions were made by Povilaitis (1960, 1966) when the generation mean analysis was used.

The failure of some of these sets of data (especially that of Raper's index II and vein angle) to satisfy the additive-dominance model could be due to the failure of one or more genetic assumptions listed by Hayman (1954) (Section 2.4.3). This is especially so for the assumptions of no multiple alleles and non-correlated gene distribution. This is because they are difficult to evaluate independently of each other. The assumptions of homozygous and diploid parents can be satisfactorily assumed since 6 of the 8 parents used for the crosses were dihaploids obtained from pollen culture studies. In addition to that, they were advance generation lines that had been selfed for several generations. Assumption of no reciprocal effect as shown by Jinks (1954), Van der Veen (1957), Van der Veen and Bink (1961), Matzinger et al. (1962), Matzinger and Mann (1962), Povilaitis (1966), and Ogilvie and Kozumplik (1980) can also be assumed to be true. However it is always possible that such assumptions might not be true for the characters and materials studied. There is a possibility that the heterogeneity within the lines and reciprocal difference do exist. These could have biased the result to some extent.

Thus it appears that there was a possibility that a more complex genetic system did exist for Raper's index II and vein angle as compared to the theoretical model proposed by Hayman (1954).

No peculiar trend of gene interaction was found when an attempt was made to describe the type of gene action from the (W_r , V_r) graphs. However there were indications that the (W_r , V_r) graphs tend to concave upwards. This was based on V_r values which were always greater than W_r values (Appendix 7). In addition to that, $\hat{b}_1$ values were generally less than unity (Tables 4.3 to 4.14). This suggested that complimentary type of interaction and/or dispersion might be responsible for the particular characters not to conform to the additive-dominance model (Allard, 1956; Mather, 1967; Coughtrey and Mather, 1970).

Of the 13 attributes which did not follow the additive-dominance model (heterogeneous ($W_r - V_r$)), only 3 did successfully follow the model when they were reanalysed based on 7 x 7 diallel data. They were wing width (12th leaf), auricle area (2nd leaf) and vein angle (2nd leaf). These 7 x 7 diallel data sets were obtained by deleting one parental array individually (parents 1 to 8) in turn. It appeared that the failure of wing width (12th leaf) to follow the model in the original data was due to the presence of parent 1 (TI 1372). Parents 7 (Kuaka 860) and 2 (HFCA 207) were responsible for the failure of auricle area (2nd leaf) and vein angle (2nd leaf) respectively.

5.2.2 Variance components estimates

For almost all characters, estimates of the additive genetic variance ($\hat{D}$) were greater than the estimates of the dominance genetic variance ($\hat{H}_1$ and $\hat{H}_2$). Extremely high values of $\hat{D}$ as compared to $\hat{H}_1$ and $\hat{H}_2$ were found in

in cases where ($W_r + V_r$) analyses of variance were not significant (i.e. presence of little non-additive genetic variance). This showed that the additive genetic variance accounted for the major proportions of total genetic variance for most of the characters. This is in agreement with other published reports on most quantitative characters in tobacco (Matzinger et al., 1960, 1962, 1966, 1971, 1972; Lamprecht, 1964, 1969, 1973; Gywn, 1966; Lamprecht and Van Wyk, 1969, 1971; Legg et al., 1970; Aycock, 1972; Jones et al., 1972; Lamprecht and Nuss, 1973; Dean, 1974; Legg and Collins, 1974). They generally showed that additive genetic (or variance of general combining ability) was the main component of total genetic variance.

However it is important to note here that even though additivity predominates in most of the characters studied, this will often be true even when much dominance of the classical type exists. This is because, the heritable portion of the continuous variation in quantitative genetic studies depends on genes which are transmitted in Mendelian fashion (i.e. classical type). These classical genetic genes are acting in polygenic systems with their effects compliment one another. These effects sometimes in simple additive fashion (i.e. additivity), but sometimes interacting in such a way that the net effect is not the sum of the effects of individual genes.

Generally it was found that both the additive genetic and dominance genetic variances were higher for the middle than the top or bottom leaves. This indicated that the environmental variance had less influence for

the middle leaves as compared to other leaf positions. This is supported by the relatively higher error variance in the top and bottom as compared to the middle leaves. Better genetic advance are thus expected if selections were made based on these leaf positions. In the case of leaf ratio, differential index and tip score, both the additive and dominance genetic variances were found to be higher in the upper leaves (2nd and 7th leaf positions) than the bottom leaves (12th and 17th leaves). An increasing predominance of additive genetic variance for the upper leaves for some characters was also reported by Humphrey et al. (1965) and Povilaitis (1964).

For some characters, namely Raper's index I, leaf dry weight, petiole length and tip score, it was found that the dominance genetic components ($\hat{H}_1$ and $\hat{H}_2$) and the resulting ratios were negative. In such cases, the estimates obtained were interpreted as estimates of small positive components or zero. This is because Brim and Cockerham (1961) stated that complete absence of dominance is very unlikely. Negative dominance components were also reported in tobacco by Robinson et al. (1954), Murty et al. (1962), Povilaitis (1964) and Dally and Robson (1969). Robinson et al. (1954) suggested that the only biological explanation is a possible existence of negative correlation between the plots. This could also be confounded by the high sampling error inherent in some particular characters (e.g. Raper's index I, leaf dry weight and petiole length).

Estimates of the genetical components of the reanalysed data were found to be slightly higher than that of the original data for wing width (12th leaf) and auricle area (2nd leaf). Smaller estimates were found in the case of vein angle (2nd leaf). In the absence of inter-locus interaction, the variance of genetical components estimated from the reanalysed data were more appropriate as compared to that of original data.

5.2.3 Further information on genetical system operating for each character

The $\sqrt{\hat{H}_1/\hat{D}}$ suggested that overdominance was found in 10 of 48 attributes. However it is important to realise that in the presence of inter-locus interactions (epistasis), the degree of dominance will be biased upwards (Comstock and Robinson, 1952; Hayman, 1954; Jinks, 1954; Lagervall, 1961).

Therefore for Raper's index I (7th and 17th leaves) where there was a strong evidence of inter-locus interaction (epistasis) present, the value obtained may be inflated from partial to overdominance. Correlated gene distribution can also bias the dominance upwards. Leffel and Hanson (1961) also pointed out that biases in estimating character values could also be responsible for inflating the apparent degree of dominance.

The $\hat{F}$ and K_D/K_R values generally showed that dominant alleles were found to be more frequent for most characters. However in some cases there were indications that dominant and recessive alleles were present in equal proportions. Recessive alleles were

more frequent for leaf ratio and leaf dry weight.

Except for the Raper's index I (2nd leaf), both indicators of the frequencies of positive and negative alleles (i.e. $\hat{F}$ and K_D/K_R values) gave similar results for all characters. The contradictory results obtained in the case of Raper's index I (2nd leaf) was probably due to the relatively smaller values of genetical components observed.

5.2.4 Graphical analysis

Even though there were variations between leaf positions, a general similarity in terms of the parental distribution of dominance was found for leaf ratio, tip score, petiole length, auricle area, vein angle, dry weight and leaf area. Parents 1, 2 and 3 were found to have the most recessive alleles. More dominant alleles were present in parents 4, 5 and 6. There was no parental array which was situated at either junction of the parabola and regression line. This implied that none of the parents contained all the dominant or recessive alleles for a particular character. In the case of Raper's index I, Raper's index II, leaf ratio and differential index, parents 6, 5 and 8 were found to contain most recessive alleles. Parents 1, 2 and 3 on the other hand contained most dominant alleles. Parental distributions of dominance for wing area were not consistent across the leaf positions. By considering only the middle leaves (7th and 12th leaves) parents 6 and 5 appeared to contain most recessive alleles. Parents 1 and 7 contained most dominant alleles. The

inconsistency of the distribution of parental lines on the (W_r, V_r) graphs across the leaf positions for this character was probably due to the presence of relatively high error variance. The genotypic to error variance ratios were low (less than unity) for all leaf positions (Table 4.1). This was supported by the relatively low heritability estimates obtained (Table 4.15).

For most characters, the analyses of variance $(W_r + V_r)$ were in agreement with the relative distribution of the (W_r, V_r) points on the regression line. In the presence of very little dominance (homogeneous $(W_r + V_r)$) the parental arrays tended to cluster together near the tangent to the parabola. However there was no actual complete absence of dominance for any character. None of the characters had all the parental arrays cluster together at the tangent to the parabola.

The (W_r, V_r) graphs for the reanalysed characters are presented in Figures 4.7.2, 4.9.2 and 4.10.2. In the presence of dominance, and no inter-locus interaction, the (W_r, V_r) points were found to be well distributed along the regression lines. The regression coefficients $(\hat{b}_1)$ were found to be greater than that of the original data and near to unity in all characters. The relative positions of the parental points along the regression lines were generally similar to that of the original data.

From the above discussions it appears that important information on the parental distribution of dominance can be obtained from the graphical analysis but not from

derived statistics approach (Sections 5.2.1, 5.2.2 and 5.2.3). As pointed by Mather and Jinks (1971, 1977) graphical analysis do also provide some information on the degree of dominance and the presence of inter-locus interaction. It is important to note however this approach is unable to estimate the proportion of dominant to recessive alleles in the parents and the consistency of the distribution of dominance across the loci. Such estimates can be obtained from the derived statistics approach.

Therefore both approaches should be used for further study if we were to get a more complete picture about the quantitative inheritance of any character. However, the derived statistics approach is more suitable for the plant breeder since the relative size of the additive and dominance genetic variances can be estimated.

5.2.5 Direction of dominance

The $((W_r + V_r), \bar{P})$ correlation coefficients were generally high and significant for most characters. This suggested that there was directional dominance in most of the characters.

Contrasting results between the two leaf-shape measurements (i.e. leaf ratio and differential index) were obtained. From the leaf ratio, wider leaf (smaller ratio) was found to be dominant to narrower leaf (larger ratio). However differential index showed that narrower leaf (smaller index) was found to be dominant. Similar results were obtained from the distribution of parental lines on the (W_r, V_r) graphs (Section 5.2.4). Parental

lines having smaller leaf ratios (i.e. wider leaves) were found to have more dominant genes. In the case of differential index, dominant genes were found in parents having narrower leaves. This disagreement however can be reconciled since they are totally two different measurements of leaf shape. Leaf ratio estimates the overall leaf shape. This was measured as the ratio of total length of midrib (i.e. including the petiole) to the maximum leaf width. On the other hand, differential index only measures the shape of the main laminar area. Even though the leaf ratio is the commonly used indicator of leaf shape (Van der Veen, 1957; Van der Veen and Bink, 1961; Chaudhry and Munshi, 1962; Sastry and Gopinath, 1969; Povilaitis, 1965; Gordon, 1969), the differential index is more appropriate estimator of leaf (laminar) shape.

Both indicators of leaf size are in good agreement with each other. Smaller leaf area and leaf dry weight were found to be dominant to the higher leaf area and leaf dry weight.

Smaller auricles (i.e. smaller area) were found to be dominant. Longer petioles, more acute angles of venation and more attenuated tips were dominant to the shorter petioles, more obtuse angles of venation and more rounded tips respectively. Consistent results were obtained from both measurements of wing size (i.e. wing width and wing area). Smaller wing area and narrower wing width were dominant to larger area and broader wing width respectively. Similar results were obtained by Van der Veen (1957), Van der Veen and Bink

(1961) and Eugechi (1971) (See section 2.3).

In discussing leaf shape, Van der Veen (1957) and Van der Veen and Bink (1961) showed that Ptpt and Pdpd genes only affected the leaf width but not the leaf length. Sinnot (1935, 1936, 1937) however proposed the concept of 'shape' as opposed to the 'dimensional' genes described by Van der Veen and Bink (1961). From his studies on family Cucurbitacea, he found that there were no genes which affected one dimension without affecting the other. The concept of dimensional genes as proposed by Van der Veen and Bink (1961) can also be used to explain the inheritance of leaf shape in this study. This is because very little variation in leaf length as compared to leaf width was observed. As a result, the variation in leaf shape observed was mainly due to the variation of only leaf width.

Based on the proposition made by Went (1951), Van der Veen and Bink (1961) suggested that the acute angle of venation, narrower leaf blade and wing width was due to the reduction of the amount of mesophyll.

The direction of dominance for the reanalysed data were found to be similar to that of the original data. However the $((W_r + V_r), \bar{P})$, correlation coefficients were generally larger than that of the original data. The higher coefficients obtained from the reanalysed data therefore strengthened the conclusion made based on the original data.

5.3 HERITABILITY ESTIMATES

The heritability estimates obtained in this study

were generally high (approximately 60 %) for leaf shape characters such as leaf ratio, vein angle, wing width, auricle area, petiole length and tip score. Moderate values (approximately 40 - 50 %) were obtained for leaf dry weight and leaf area. The values obtained were consistent to those reported by Matzinger et al., 1966 1972; Matzinger, 1968; Legg and Collins, 1971a, 1971b, 1975; Lamprecht and Nuss, 1973). For most of these characters, they found that the narrow-sense heritability estimates were moderate to high in value. The narrow-sense heritabilities were mostly used since they are more appropriate for self-pollinated crop like tobacco. In addition to that quantitative genetic studies in tobacco generally showed that additive genetic variance is the main component of genetic variance. Similar trends were also observed for the characters studied in this thesis.

The relatively high narrow-sense heritability obtained for the leaf:shape characters suggested that environmental influence had very little importance in these characters. This implied that reasonable progress could be achieved if selection for these characters were made.

The higher heritability estimates observed for wing width as compared to the wing area suggested that wing width is a more reliable indicator of wing size than wing area. Similar results were obtained from the estimates of genetical components. The relative sizes of genetical components to error variance were higher for the wing width.

Across the leaf positions, it was generally found that the estimates were higher for the middle (7th and 12th leaves) than the top (2nd leaf) or bottom (17th leaf) leaf. This is again consistent with the components of genetic variation discussed in Section 5.2.2.

The negative estimates obtained for some characters were the artifacts of sampling error and were taken to be zero or very low values.

5.4 HETEROSIS

Very little heterosis was observed for leaf area and leaf dry weight. This low level of heterosis in the hybrids mainly due to the fact that the parental lines used in the crosses has a narrow genetic base. The dihaploid parents used in the crosses arose from the same genetic base.

Little heterosis was consistent with the results of the variance component estimate. Dominance was found to be of minor importance for both of these characters.

Similar results were also obtained by other workers. For the characters reported, increased heterosis was due to the increased genetic diversity of the parents (Matzinger and Wernsman, 1967, 1968; Van der Berg and Matzinger, 1970; Povilaitis, 1971). They also showed that the wider the phenotypic mean between the parents, the greater the chance of obtaining significant heteroitic effects. Little or no heterosis

were generally observed by them. As a result the advantages of the flue-cured tobacco hybrids over the existing varieties have not been demonstrated sufficiently to warrant the additional cost of seed production.

5.5 CORRELATION STUDIES

When several important characters are required in the evaluation of the genotypes, it is necessary to determine the correlations between these characters. This understanding will aid the plant breeder in deciding what are the characters to be used as the basis of selection. As an example a high correlation coefficient between leaf dry weight and leaf area ($r_p = 0.69$ to 0.82 , $r_G = 0.78$ to 0.89) and highly significant implied that either of these can be used to select for larger leaves. However if a choice has to be made between the two, the one with the higher heritability would be preferred. In this case, leaf area should be used since the heritability estimates were higher than those of leaf dry weight. This was especially so when the selection based on the middle leaves was used. The heritability estimates were found to be higher in the middle leaves as compared to other leaf positions. In addition to that the leaf area is much easier to estimate than the leaf dry weight. Leaf area can be estimated by using non-destructive linear measurements such as leaf length and leaf width. (Tejwani et al., 1957; Suggs et al., 1960; McKee and Yocum, 1970; Raper et al., 1974). Leaf area can also be estimated from the plant stem diameter (Splinter and Beeman, 1968).

In cases where the objective of the breeding programme is to increase the phenotypic mean for more than one character, positive and high correlation coefficients between these characters are desirable. For example positive and high correlation coefficients between leaf area and leaf dry weight suggested that considerable progress under selection for these characters can be achieved simultaneously.

Narrow leaf was found to be significantly associated with more attenuated tip, longer petiole, smaller vein angle, smaller leaf area, smaller leaf dry weight and narrower wing width. Similar results were obtained from qualitative inheritance studies reported by Van der Veen (1957) and Van der Veen and Bink (1961).

Generally it was observed that the genotypic correlation coefficients were highly significant and in the same direction. Therefore the phenotypic correlation coefficients do provide some information on the genetic make up of the association between these characters.

5.6 PLANT BREEDING ASPECTS

5.6.1 Diallel analysis

As discussed by Hayman (1954), an accurate genetic interpretation of diallel analysis based on Jinks-Hayman model can be made only when all the genetical assumptions are true. However such assumptions are very difficult to completely satisfy. This is especially so with respect to the independent distribution of genes and the absence of epistasis. Thus

the genetical interpretations for Raper's index II (7th and 17th leaves) and vein angle (2nd leaf) could be biased since there were indications that inter-locus interactions (epistasis) were present.

It has been shown that the failure of some of these assumptions will affect the (W_r , V_r) graphs and some of the genetical interpretations such as the degree of dominance. Therefore, the dominance observed could be biased upwards for Raper's index II since there were indications of inter-locus interaction present. Even though tests are available where the presence of epistasis can be shown (Hayman, 1954), the diallel analysis procedures were not able to partition their effect as in Hayman's generation mean analysis (Hayman, 1958, 1960b). In generation mean analysis, the genetical components can be partitioned into the additive, dominance and epistatic effects. Therefore, for Raper's index II (7th and 17th leaves) and vein angle (2nd leaf) it might be useful to carry out generation mean analyses. The relative size of dominance and additive in relation to the epistatic effects can be estimated. However more experimental work is involved since it requires at least two filial generations together with some generations of back-crosses.

Despite the disadvantages, such as the large amount of F_1 seeds needed, together with the failure of some of the assumptions, the use of diallel analyses in plant breeding programmes is still very popular. This is

especially so for crops like tobacco (used in this study) where a large amount of F_1 hybrids can be easily obtained. The main advantage of diallel analysis is that breeding materials can be screened from early stages. The performance of the progeny and the appropriate breeding programmes to be carried out can be predicted. This can be carried out either by the procedures of Jinks-Hayman or that of Griffing (Griffing, 1956).

Even though Jinks-Hayman's analyses do provide extra information about the genetical systems of the plant materials studied, the one proposed by Griffing (1956) provides sufficient information for the practical breeder. This is especially so in cases where epistasis and/or correlated gene distribution are present. It has been shown that the presence of correlated gene distribution has no effect on the specific and combining ability estimates (Nassar, 1965). The presence of epistasis was included in the model (Matzinger and Kempthorne, 1956; Griffing, 1956).

5.6.2 Tobacco breeding programme

The main objectives in a flue-cured tobacco breeding programme are high yield, resistance to pests and diseases, and high quality. Breeding for adaptation to mechanical harvesting is also important.

A number of techniques can be used in tobacco breeding programmes and these include the use of various selection methods, dihaploids, interspecific hybridisation and F_1 hybrids. Some of these techniques

were given by Allard (1960), Poehlman (1979) and Simmonds (1979). The pedigree breeding together with newer concepts such as recurrent selection have been shown to be reliable means of developing new cultivars in tobacco. This is mainly due to the fact that in most quantitative characters in tobacco, the additive genetic variance is the main component of total genetic variance. Similar results were also obtained for all the characters currently studied. The use of F_1 hybrids as a means of producing new cultivars from the materials studied is also not justified since very little hybrid vigour was observed for leaf area and leaf dry weight.

A high additive genetic variance together with high narrow sense heritability estimates for most of the characters indicated that a considerable genetic advance can be expected.

The high genotypic and phenotypic correlation coefficients and in the same direction for most pairs of characters indicated that either one can be used as a criterion of selection. However, the use of genotypic correlation coefficient is more appropriate since it deals with the variations that are genetically transmissible from one generation to another.

6. CONCLUSIONS

1. A high genetic variability was observed for almost all characters and leaf positions in the materials studied.
2. Generally epistasis were relatively less important for most characters. Most of the observed genetic variability was attributed to additive and dominance effects of genes.
3. Additive genetic variance was the main component of the total genetic variance for most characters. The variance due to the dominance effects were much less. This agreed with most quantitative studies reported on tobacco. Even though in some characters the additive effect of genes were more prominent in the upper leaves as compared to other leaf positions, it was generally found that the additive component was highest in the middle leaves. A similar trend was observed also for the dominance effects.
4. The estimated narrow and broadsense heritabilities obtained ranged from moderate to moderately high for most characters. The values were higher in the middle leaves as compared to other leaf positions.
5. Very little hybrid vigour was observed for both the leaf area and leaf dry weight. The F_1 hybrids were significantly different from the mid-parental values only for a few cross combinations. No particular trend was observed across the leaf positions.
6. Both the phenotypic and genotypic correlation

coefficients were generally high (approximately 0.6) and significant for most pairs of characters. The two correlation types generally were in agreement with one another in terms of the characters' trends of correlation values and levels of significance.

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APPENDIX 1

DERIVATIONS OF THE VARIANCE COMPONENTS ESTIMATES
FOR HALF DIALLEL MODEL FROM MATHER AND JINKS FULL
DIALLEL MODEL (Mather and Jinks, 1971)

The model for the Second Degree Statistics for full diallel (Mather and Jinks, 1971):

$$V_p = D + E_p$$

$$V_{\bar{r}} = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}H_2 - \frac{1}{4}F + \left(\frac{1}{2}\right)\frac{(n-2)}{n^2}E_F + \frac{1}{n^2}E_p$$

$$\bar{W}_r = \frac{1}{2}D - \frac{1}{4}F + E_p/n$$

$$\bar{V}_r = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + \left(\frac{1}{2}\right)\frac{(n-1)}{n}E_F + (E_p/n)$$

where V_p = variance of the parents

$V_{\bar{r}}$ = variance of the array mean

$\bar{W}_r$ = mean of array covariance

$\bar{V}_r$ = mean of array variance

E_p = error variance of the parents

E_F = error variance of the hybrids.

The error component for the hybrids were multiplied by factor $(\frac{1}{2})$ since the two sets of reciprocals were first averaged before these statistics were computed (Mather and Jinks, 1971). In the case of $\frac{1}{2}$ diallel where only one set of hybrids were obtained, therefore the following model should be used:

$$V_p = D + E_p$$

$$V_{\bar{r}} = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}H_2 - \frac{1}{4}F + \frac{(n-2)}{n^2}E_p + (E_p/n^2)$$

$$\bar{W}_r = \frac{1}{2}D - \frac{1}{4}F + E_p/n$$

$$\bar{V}_r = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + \frac{(n-1)}{n}E_p + (E_p/n)$$

These relationships were then simultaneously solved to obtain the variance component estimate as follows:

1) $\hat{D}$:

$$V_p = D + E_p$$

$$\text{Therefore } D = V_p - E_p$$

2) $\hat{H}_1$:

$$\bar{W}_r = \frac{1}{2}D - \frac{1}{4}F + \frac{1}{2}nE_p$$

$$\bar{V}_r = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + \frac{(n-1)}{n}E_F + (E_p/n)$$

$$\bar{V}_r - \bar{W}_r = -\frac{1}{4}(V_p - E_p) + \frac{1}{4}H_1 + \frac{n-1}{n}E_F$$

$$4\bar{V}_r - 4\bar{W}_r = -V_p + E_p + H_1 + \frac{4(n-1)}{n}E_F$$

$$H_1 = 4\bar{V}_r - 4\bar{W}_r + V_p - \frac{4n}{n}E_F - E_p$$

3) $\hat{H}_2$:

$$V\bar{r} = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}H_2 - \frac{1}{4}F + \frac{(n-1)}{n^2}E_F + (E_p/n^2)$$

$$\bar{V}_r = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + \frac{(n-1)}{n}E_F + E_p/n$$

$$\bar{V}_r - V\bar{r} = \frac{1}{4}H_2 + \left(\frac{n-1}{n} - \frac{n-1}{n^2}\right)E_F + \left(\frac{1}{n} - \frac{1}{n^2}\right)E_p$$

$$= \frac{1}{4}H_2 + \frac{(n-1)^2}{n^2}E_F + \frac{4(n-1)}{n^2}E_p$$

$$H_2 = 4\bar{V}_r - 4V\bar{r} - 4\left(\frac{(n-1)^2}{n^2}\right)E_F - \frac{4(n-1)}{n^2}E_p$$

4) $\hat{F}$:

$$D = V_p - E_p \text{-----(1)}$$

$$\bar{W}_r = \frac{1}{2}D - \frac{1}{4}F + (E_p/n) \text{-----(2)}$$

Substitute (1) in (2)

$$\frac{1}{4}F = \frac{1}{2}D - \bar{W}_r + (E_p/n)$$

$$F = 2(V_p - E_p) - 4\bar{W}_r + (4E_p/n)$$

$$= 2V_p - 4\bar{W}_r - \frac{2(2-n)}{n}E_p$$

When $E_{\text{pool}} = E_F = E_p$, the following relationship were obtained:

$$\hat{D} = V_p - E_{\text{pool}}$$

$$\hat{H}_1 = 4\overline{Vr} - 4\overline{Wr} + V_p - \frac{5n-4}{n} E_{\text{pool}}$$

$$\hat{H}_2 = 4\overline{Vr} - 4\overline{Vr} - \left(\frac{4(n-1)}{n}\right) E_{\text{pool}}$$

$$\hat{F} = 2V_p - 4\overline{Wr} - \frac{2(n-2)}{n} E_{\text{pool}}$$

APPENDIX 2 THE LISTING OF THE COMPUTER PROGRAMME WRITTEN TO ESTIMATE THE Vr
(ARRAY VARIANCE) AND Wr (ARRAY PARENT-OFFSPRING COVARIANCE)

86700 FORTRAN COMPILATION MARK 3.0.140 TUESDAY

V R W R
= = = =

FILE	8(TITLE="DIALI/TOT ",KIND=DISK,FILETYPE=7)	C	00000C01
FILE	9(TITLE="VRWR/TOTPAKR",KIND=DISK,MAXRECSIZE=16,BLOCKSIZE=480)	C	00000C02
			START OF SE
	DIMENSION XIN(8,8), SPAR(1), PARM(1), VPAR(1),	C	002:0C00
1	SARR(8), ARRM(8), ARRSO(8), SCRPRU(8),	C	002:0C00
2	VARR(8), WARR(8), WRFVR(8), WRMVVR(8), PARR(8)	C	002:0C00
	DO 70 I=1,1248,8	C	002:0C00
	DO 4 L=1,8	C	002:0C01
4	READ(8,5)(XIN(M,L),N=1,8)	C	002:0C02
5	FORMAT(8F8.2)	C	002:0C12
C		C	002:0C12
	SPAR(1)=XIN(1,1)+XIN(2,2)+XIN(3,3)+XIN(4,4)	C	002:0C12
1	+XIN(5,5)+XIN(6,6)+XIN(7,7)+XIN(8,8)	C	002:0C16
	VPAR(1)=(XIN(1,1)**2+XIN(2,2)**2+XIN(3,3)**2+XIN(4,4)**2	C	002:0C19
1	+XIN(5,5)**2+XIN(6,6)**2+XIN(7,7)**2+XIN(8,8)**2)/7.0	C	002:0C1E
2	-(SPAR(1)**2/56.0)	C	002:0C23
	PARM(1)=SPAR(1)/8.0	C	002:0C25
	SARR(1)=XIN(1,1)+XIN(2,1)+XIN(3,1)+XIN(4,1)	C	002:0C27
1	+XIN(5,1)+XIN(6,1)+XIN(7,1)+XIN(8,1)	C	002:0C2A
	SARR(2)=XIN(2,1)+XIN(2,2)+XIN(3,2)+XIN(4,2)	C	002:0C2E
1	+XIN(5,2)+XIN(6,2)+XIN(7,2)+XIN(8,2)	C	002:0C31
	SARR(3)=XIN(3,1)+XIN(3,2)+XIN(3,3)+XIN(4,3)	C	002:0C35
1	+XIN(5,3)+XIN(6,3)+XIN(7,3)+XIN(8,3)	C	002:0C39
	SARR(4)=XIN(4,1)+XIN(4,2)+XIN(4,3)+XIN(4,4)	C	002:0C3L
1	+XIN(5,4)+XIN(6,4)+XIN(7,4)+XIN(8,4)	C	002:0C40
	SARR(5)=XIN(5,1)+XIN(5,2)+XIN(5,3)+XIN(5,4)	C	002:0C44
1	+XIN(5,5)+XIN(6,5)+XIN(7,5)+XIN(8,5)	C	002:0C48
	SARR(6)=XIN(6,1)+XIN(6,2)+XIN(6,3)+XIN(6,4)	C	002:0C4C
1	+XIN(6,5)+XIN(6,6)+XIN(7,6)+XIN(8,6)	C	002:0C4F
	SARR(7)=XIN(7,1)+XIN(7,2)+XIN(7,3)+XIN(7,4)	C	002:0C53
1	+XIN(7,5)+XIN(7,6)+XIN(7,7)+XIN(8,7)	C	002:0C57
	SARR(8)=XIN(8,1)+XIN(8,2)+XIN(8,3)+XIN(8,4)	C	002:0C5B
1	+XIN(8,5)+XIN(8,6)+XIN(8,7)+XIN(8,8)	C	002:0C5E

C	ARRSQ(1)=XIN(1,1)**2+XIN(2,1)**2+XIN(3,1)**2+XIN(4,1)**2	C	00022:00062
1	+XIN(5,1)**2+XIN(6,1)**2+XIN(7,1)**2+XIN(8,1)**2	C	00022:00062
1	ARRSQ(2)=XIN(2,1)**2+XIN(2,2)**2+XIN(3,2)**2+XIN(4,2)**2	C	00022:00062
1	+XIN(5,2)**2+XIN(6,2)**2+XIN(7,2)**2+XIN(8,2)**2	C	00022:00062
1	ARRSQ(3)=XIN(3,1)**2+XIN(3,2)**2+XIN(3,3)**2+XIN(4,3)**2	C	00022:00062
1	+XIN(5,3)**2+XIN(6,3)**2+XIN(7,3)**2+XIN(8,3)**2	C	00022:00062
1	ARRSQ(4)=XIN(4,1)**2+XIN(4,2)**2+XIN(4,3)**2+XIN(4,4)**2	C	00022:00062
1	+XIN(5,4)**2+XIN(6,4)**2+XIN(7,4)**2+XIN(8,4)**2	C	00022:00062
1	ARRSQ(5)=XIN(5,1)**2+XIN(5,2)**2+XIN(5,3)**2+XIN(5,4)**2	C	00022:00062
1	+XIN(5,5)**2+XIN(6,5)**2+XIN(7,5)**2+XIN(8,5)**2	C	00022:00062
1	ARRSQ(6)=XIN(6,1)**2+XIN(6,2)**2+XIN(6,3)**2+XIN(6,4)**2	C	00022:00062
1	+XIN(6,5)**2+XIN(6,6)**2+XIN(7,6)**2+XIN(8,6)**2	C	00022:00062
1	ARRSQ(7)=XIN(7,1)**2+XIN(7,2)**2+XIN(7,3)**2+XIN(7,4)**2	C	00022:00062
1	+XIN(7,5)**2+XIN(7,6)**2+XIN(7,7)**2+XIN(8,7)**2	C	00022:00062
1	ARRSQ(8)=XIN(8,1)**2+XIN(8,2)**2+XIN(8,3)**2+XIN(8,4)**2	C	00022:00062
1	+XIN(8,5)**2+XIN(8,6)**2+XIN(8,7)**2+XIN(8,8)**2	C	00022:00062
C	SCRPRU(1)=XIN(1,1)*XIN(1,1)+XIN(2,1)*XIN(2,2)	C	00022:00062
1	+XIN(3,1)*XIN(3,3)+XIN(4,1)*XIN(4,4)	C	00022:00062
1	+XIN(5,1)*XIN(5,5)+XIN(6,1)*XIN(6,6)	C	00022:00062
1	+XIN(7,1)*XIN(7,7)+XIN(8,1)*XIN(8,8)	C	00022:00062
1	SCRPRU(2)=XIN(2,1)*XIN(1,1)+XIN(2,2)*XIN(2,2)	C	00022:00062
1	+XIN(3,2)*XIN(3,3)+XIN(4,2)*XIN(4,4)	C	00022:00062
1	+XIN(5,2)*XIN(5,5)+XIN(6,2)*XIN(6,6)	C	00022:00062
1	+XIN(7,2)*XIN(7,7)+XIN(8,2)*XIN(8,8)	C	00022:00062
1	SCRPRU(3)=XIN(3,1)*XIN(1,1)+XIN(3,2)*XIN(2,2)	C	00022:00062
1	+XIN(3,3)*XIN(3,3)+XIN(4,3)*XIN(4,4)	C	00022:00062
1	+XIN(5,3)*XIN(5,5)+XIN(6,3)*XIN(6,6)	C	00022:00062
1	+XIN(7,3)*XIN(7,7)+XIN(8,3)*XIN(8,8)	C	00022:00062
1	SCRPRU(4)=XIN(4,1)*XIN(1,1)+XIN(4,2)*XIN(2,2)	C	00022:00062
1	+XIN(4,3)*XIN(3,3)+XIN(4,4)*XIN(4,4)	C	00022:00062
1	+XIN(5,4)*XIN(5,5)+XIN(6,4)*XIN(6,6)	C	00022:00062
1	+XIN(7,4)*XIN(7,7)+XIN(8,4)*XIN(8,8)	C	00022:00062
1	SCRPRU(5)=XIN(5,1)*XIN(1,1)+XIN(5,2)*XIN(2,2)	C	00022:00062
1	+XIN(5,3)*XIN(3,3)+XIN(5,4)*XIN(4,4)	C	00022:00062
1	+XIN(5,5)*XIN(5,5)+XIN(6,5)*XIN(6,6)	C	00022:00062
1	+XIN(7,5)*XIN(7,7)+XIN(8,5)*XIN(8,8)	C	00022:00062
1	SCRPRU(6)=XIN(6,1)*XIN(1,1)+XIN(6,2)*XIN(2,2)	C	00022:00062
1	+XIN(6,3)*XIN(3,3)+XIN(6,4)*XIN(4,4)	C	00022:00062
1	+XIN(6,5)*XIN(5,5)+XIN(6,6)*XIN(6,6)	C	00022:00062
1	+XIN(7,6)*XIN(7,7)+XIN(8,6)*XIN(8,8)	C	00022:00062
1	SCRPRU(7)=XIN(7,1)*XIN(1,1)+XIN(7,2)*XIN(2,2)	C	00022:00062
1	+XIN(7,3)*XIN(3,3)+XIN(7,4)*XIN(4,4)	C	00022:00062
1	+XIN(7,5)*XIN(5,5)+XIN(7,6)*XIN(6,6)	C	00022:00062
1	+XIN(7,7)*XIN(7,7)+XIN(8,7)*XIN(8,8)	C	00022:00062
1	SCRPRU(8)=XIN(8,1)*XIN(1,1)+XIN(8,2)*XIN(2,2)	C	00022:00062
1	+XIN(8,3)*XIN(3,3)+XIN(8,4)*XIN(4,4)	C	00022:00062
1	+XIN(8,5)*XIN(5,5)+XIN(8,6)*XIN(6,6)	C	00022:00062
1	+XIN(8,7)*XIN(7,7)+XIN(8,8)*XIN(8,8)	C	00022:00062

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..C

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PARR(1)=XIN(1,1)
PARR(2)=XIN(2,2)
PARR(3)=XIN(3,3)
PARR(4)=XIN(4,4)
PARR(5)=XIN(5,5)
PARR(6)=XIN(6,6)
PARR(7)=XIN(7,7)
PARR(8)=XIN(8,8)
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C

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DO 10 L=1,8
ARRM(L)=SARR(L)/8.0
VARR(L)=ARRSQ(L)/7.0-(SARR(L)**2)/56.0
WARR(L)=SCRPR(L)/7.0-(SARR(L)*SPAR(1))/56.0
WRPVR(L)=WARR(L)+VARR(L)
10 WRMVR(L)=WARR(L)-VARR(L)
DO 60 L=1,8
60 WRITE(9,65)ARRM(L),VARR(L),WARR(L),
1 WRPVR(L),WRMVR(L),VPAR(1),PARR(L)
65 FORMAT(F8.4,6F13.4)
70 CONTINUE
LOCK 9
END
```

```
C 002:0122:
CC 002:0122:
CC 002:0123:
CC 002:0125:
CC 002:0126:
CC 002:0128:
CC 002:012A:
CC 002:012B:
CC 002:012D:
CC 002:012F:
CC 002:0130:
CC 002:0132:
CC 002:0137:
CC 002:013C:
CC 002:0140:
CC 002:0146:
CC 002:0147:
CC 002:0150:
CC 002:015U:
CC 002:015U:
CC 002:0160:
CC 002:0161:
```

SEGMENT 002 IS

#####

FORMAT SEGMENT
START OF SE
SEGMENT 006 IS

```
NO ERRORS DETECTED. NUMBER OF CARDS = 105.
COMPILATION TIME = 12 SECONDS ELAPSED, 2.83 SECONDS PROCESSING.
O2 STACK SIZE = 19 WORDS. FILESIZE = 960 WORDS. ESTIMATED CORE STORAGE REQUIREMENT = 15
TOTAL PROGRAM CODE = 454 WORDS. ARRAY STORAGE = 139 WORDS.
NUMBER OF PROGRAM SEGMENTS = 7. NUMBER OF DISK SEGMENTS = 29.
PROGRAM CODE FILE = (AGU173YAACUB)VRWR UN PACK.
COMPILER COMPILED ON 10/31/78 (FORTRAN UN PACK).
```

APPENDIX 3 THE LISTING OF THE COMPUTER PROGRAMME WRITTEN TO ESTIMATE THE SECOND
DEGREE STATISTICS, GENETICAL COMPONENTS, RATIOS OF GENETICAL COMPONENTS
AND HERITABILITY ESTIMATES

D6700 F U R T R A N C O M P I L A T I O N M A R K 3.0.140 WEDNESDAY

G E N C O M

= = = = =

```

FILE 8(TITLE="VRWR/TOTPARR", KIND=DISK, FILETYPE=7)
FILE 9(TITLE="GENCOM/TOT/ETOT", KIND=DISK,
1      MAXRECSIZE=18, BLOCKSIZE=540)
FILE 10(TITLE="SESTAT/TOT/ETOT", KIND=DISK,
1      MAXRECSIZE=15, BLOCKSIZE=450)
FILE 11(TITLE="ERROR/TOT", KIND=DISK, FILETYPE=7)

DIMENSION XIN(5,8), ARRVRM(1), ARRHRM(1), SCFARM(1), SUARRM(1),
1      VARRYM(1), VPAR(1), C(1), H1(1), H2(1),
2      F(1), RTH1D(1), UV(1), H2N(1), H2B(1), HDRAT(1),
3      ERR(3,3), EPAR(1), EFAM(1), ETOT(1), DRRAT(1)
DO 70 I=1,52
DO 4 L=1,8
4 READ(6,5)(XIN(M,L),M=1,4)
5 FORMAT(F8.4,2F13.4,26X,F13.4)
DO 10 L=1,1
10 READ(11,20)(ERR(M,L),M=1,3)
20 FORMAT(3X,3F10.4)

SECOND DEGREE STATISTICS
1 ARRVRM(1)=(XIN(2,1)+XIN(2,2)+XIN(2,3)+XIN(2,4)
+XIN(2,5)+XIN(2,6)+XIN(2,7)+XIN(2,8))/8.0
1 ARRHRM(1)=(XIN(3,1)+XIN(3,2)+XIN(3,3)+XIN(3,4)
+XIN(3,5)+XIN(3,6)+XIN(3,7)+XIN(3,8))/8.0
1 SCFARM(1)=(XIN(1,1)**2+XIN(1,2)**2+XIN(1,3)**2+XIN(1,4)**2
+XIN(1,5)**2+XIN(1,6)**2+XIN(1,7)**2+XIN(1,8)**2)
1 SUARRM(1)=(XIN(1,1)+XIN(1,2)+XIN(1,3)+XIN(1,4)
+XIN(1,5)+XIN(1,6)+XIN(1,7)+XIN(1,8))
1 VARRYM(1)=SCFARM(1)/7.0-(SUARRM(1)**2)/56.0
VPAR(1)=XIN(4,1)
EPAR(1)=ERR(3,1)
EFAM(1)=ERR(2,1)
ETOT(1)=ERR(1,1)

```

C
C
C

```

C 00000001
C 00000002
C 00000003
C 00000004
C 00000005
C 00000006
C START OF S
C 002:0000
C 002:0000
C 002:0000
C 002:0000
C 002:0001
C 002:0002
C 002:0012
C 002:0012
C 002:0014
C 002:0024
C 002:0024
C 002:0024
C 002:0024
C 002:0027
C 002:002C
C 002:002F
C 002:0033
C 002:0038
C 002:003D
C 002:0041
C 002:0044
C 002:0048
C 002:0049
C 002:004B
C 002:004C

```


CC

THE GENETIC COMPONENTS

```

D(1)=VPAK(1)-ETOT(1)
H1(1)=ARRVRM(1)*4.0+VPAK(1)-ARRWRM(1)*4.0-ETOT(1)*3.5-ETOT(1)
H2(1)=ARRVRM(1)*4.0-VARKYM(1)*4.0-ETOT(1)*3.0625-ETOT(1)*0.4375
F(1)=VPAK(1)*2-ARRWRM(1)*4.0-ETOT(1)*1.500
RTH1D(1)=SQRT(ABS(H1(1)/D(1)))
UV(1)=(H2(1)/H1(1))/4.0
H2N(1)=(D(1)*0.5+H1(1)*0.5-H2(1)*0.5-F(1)*0.5)*100
1 / (D(1)*0.5+H1(1)*0.5-H2(1)*0.25-F(1)*0.5+ETOT(1))
H2B(1)=(D(1)*0.5+H1(1)*0.5-H2(1)*0.25-F(1)*0.5)*100
1 / (D(1)*0.5+H1(1)*0.5-H2(1)*0.25-F(1)*0.5+ETOT(1))
HDRAT(1)=F(1)*0.5/(SQRT(ABS(D(1)*(H1(1)-H2(1))))))
1 DRRAT(1)=(SQRT(ABS(4*D(1)*H1(1)))+F(1))/
1 (SQRT(ABS(4*D(1)*H1(1)))-F(1))
DO 50 J=1,1
50 WRITE(10,55)VPAK(1),ARRVRM(1),ARRWRM(1),VARKYM(1),ETOT(1),DRRAT(1)
55 FORMAT(6F12.4)
DO 60 L=1,1
60 WRITE(9,65)D(1),H1(1),H2(1),F(1),ETOT(1),RTH1D(1),UV(1),HDRAT(1),
1 H2N(1),H2B(1)
65 FORMAT(SF13.4,3F8.4,2F8.2)
70 CONTINUE
LOCK 9
LOCK 10
END

```

MAGLEY UNIVERSITY

SEGMENT 002 IS

FORMAT SEGMENT
START OF S
SEGMENT 007 IS

NO ERRORS DETECTED. NUMBER OF CARDS = 60.
 COMPILATION TIME = 20 SECONDS ELAPSED, 1.85 SECONDS PROCESSING.
 L2 STACK SIZE = 29 WORDS. FILE SIZE = 1980 WORDS. ESTIMATED CORE STORAGE REQUIREMENT =
 TOTAL PROGRAM CODE = 350 WORDS. ARRAY STORAGE = 68 WORDS.
 NUMBER OF PROGRAM SEGMENTS = 8. NUMBER OF DISK SEGMENTS = 30.
 PROGRAM CODE FILE = (AGU173YAACUB) GENCOM ON PACK.
 COMPILER COMPILED ON 10/31/78 (FORTRAN UN PACK).

APPENDIX 4

ANALYSES OF VARIANCE FOR BOTH THE 8 x 8 ORIGINAL
DATA AND 7 x 7 REANALYSED
DATA

1. LEAF RATIO

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	1.5246	0.90	NS
GENOTYPES	35	20.5712	12.21	****
ERROR	70	1.6849		
COEFF. OF VAR. = 0.23 STD. ERROR = 0.75				
STD. DEVIATION = 1.29				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.0656	0.22	NS
GENOTYPES	35	4.1781	14.32	****
ERROR	70	0.2917		
COEFF. OF VAR. = 0.44				
STD. DEVIATION = 0.54 STD. ERROR = 0.31				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.2008	1.74	NS
GENOTYPES	35	1.9372	16.82	****
ERROR	70	0.1152		
COEFF. OF VAR. = 0.12 STD. ERROR = 0.16				
STD. DEVIATION = 33.94				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.7052	6.84	***
GENOTYPES	35	1.0277	9.98	****
ERROR	70	0.1030		
COEFF. OF VAR. = 0.14 STD. ERROR = 0.26				
STD. DEVIATION = 0.32				

2. DIFFERENTIAL INDEX

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.1768	0.14	NS
GENOTYPES	35	8.1531	6.26	
ERROR	70	1.3023		
COEFF. OF VAR. = 0.32		STD. ERROR = 0.66		
STD. DEVIATION = 1.14				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	9.0555	13.46	****
GENOTYPES	35	2.4953	3.7	****
ERROR	70	0.6725		
COEFF. OF VAR. = 0.21 STD. ERROR = 0.47 STD. DEVIATION = 0.82				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	1.2018	2.12	NS
GENOTYPES	35	1.7730	3.13	****
ERROR	70	0.5662		
COEFF. OF VAR. = 0.19 STD. ERROR = 0.43 STD. DEVIATION = 0.75				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	1.3260	1.75	NS
GENOTYPES	35	1.4239	1.88	*
ERROR	70	0.7569		
COEFF. OF VAR. = 0.19 STD. ERROR = 0.50 STD. DEVIATION = 0.87				

3. RAPER'S INDEX I

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.0471	0.43	NS
GENOTYPES	35	0.1956	1.80	*
ERROR	70	0.1086		
COEFF. OF VAR. = 0.13 STD. ERROR = 0.19				
STD. DEVIATION = 0.33				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.1309	1.06	NS
GENOTYPES	35	0.4323	3.49	****
ERROR	70	0.1239		
COEFF. OF VAR. = 0.16				
STD. DEVIATION = 0.35 STD. ERROR = 0.29				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.05877	2.10	NS
GENOTYPES	35	0.10432	3.72	****
ERROR	70	0.02801		
COEFF. OF VAR. = 0.08				
STD. DEVIATION = 0.17 STD. ERROR = 0.10				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.03943	1.59	NS
GENOTYPES	35	0.05753	2.32	***
ERROR	70	0.02478		
COEFF. OF VAR. = 0.08				
STD. DEVIATION = 0.16 STD. ERROR = 0.13				

4. RAPER'S INDEX II

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	1.8992	1.43	NS
GENOTYPES	35	11.3559	8.58	****
ERROR	70	1.3238		
COEFF. OF VAR. = 0.30 STD. ERROR = 0.66 STD. DEVIATION = 1.15				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	5.3097	2.60	NS
GENOTYPES	35	18.8994	9.24	****
ERROR	70	2.0461		
COEFF. OF VAR. = 0.37 STD. ERROR = 0.83 STD. DEVIATION = 1.43				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	1.0423	0.66	NS
GENOTYPES	35	7.8563	4.98	****
ERROR	70	1.5765		
COEFF. OF VAR. = 0.32 STD. ERROR = 0.72 STD. DEVIATION = 1.26				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	2.9955	3.25	*
GENOTYPES	35	8.6605	9.40	****
ERROR	70	0.9214		
COEFF. OF VAR. = 0.20 STD. ERROR = 0.55 STD. DEVIATION = 0.10				

5. TIP SCORE

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.2128	3.47	*
GENOTYPES	35	0.9770	15.95	****
ERROR	70	0.0613		
COEFF. OF VAR. = 0.07 STD. ERROR = 0.14				
STD. DEVIATION = 0.25				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.2769	4.62	*
GENOTYPES	35	1.0477	17.46	****
ERROR	70	0.0600		
COEFF. OF VAR. = 0.07				
STD. DEVIATION = 0.24 STD. ERROR = 0.14				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.0889	0.90	NS
GENOTYPES	35	1.0401	10.48	****
ERROR	70	0.0992		
COEFF. OF VAR. = 0.10 STD. ERROR = 0.18				
STD. DEVIATION = 0.32				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.2086	2.06	NS
GENOTYPES	35	0.7856	7.75	****
ERROR	70	0.1013		
COEFF. OF VAR. = 0.11 STD. ERROR = 0.18				
STD. DEVIATION = 0.32				

6. PETIOLE LENGTH

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	463.69	0.77	NS
GENOTYPES	35	1810.69	3.01	****
ERROR	70	600.56		
COEFF. OF VAR. = 0.62 STD. ERROR = 14.15 STD. DEVIATION = 24.51				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	327.29	2.26	NS
GENOTYPES	35	2007.41	13.83	****
ERROR	70	145.11		
COEFF. OF VAR. = 0.17 STD. ERROR = 6.95 STD. DEVIATION = 12.05				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	626.18	3.41	*
GENOTYPES	35	2627.53	14.31	****
ERROR	70	183.60		
COEFF. OF VAR. = 0.14 STD. ERROR = 7.82 STD. DEVIATION = 13.55				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	133.10	0.55	NS
GENOTYPES	35	1896.30	7.86	****
ERROR	70	241.30		
COEFF. OF VAR. = 0.15 STD. ERROR = 8.97 STD. DEVIATION = 15.53				

7. WING WIDTH

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	65.5093	0.65	NS
GENOTYPES	35	1060.1735	10.55	****
ERROR	70	100.5188		
COEFF. OF VAR. = 0.39 STD. ERROR = 5.79				
STD. DEVIATION = 10.03				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	48.2593	0.80	NS
GENOTYPES	35	1342.7712	22.30	****
ERROR	70	60.2116		
COEFF. OF VAR. = 0.19 STD. ERROR = 4.48				
STD. DEVIATION = 7.76				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	22.9537	0.19	NS
GENOTYPES	35	1683.4537	13.83	****
ERROR	70	118.4775		
COEFF. OF VAR. = 0.30 STD. ERROR = 6.28 STD. DEVIATION = 10.88				

12th Leaf (7 x 7 reanalysed diallel data)

SOURCE	DF	MS	F	SIG.
BLOCKS	2	104.6190	1.24	NS
GENOTYPES	27	1760.2306	20.78	****
ERROR	54	84.7055		
COEFF. OF VAR. = 0.26 STD. ERROR = 5.31 STD. DEVIATION = 9.20				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	10.9537	0.10	NS
GENOTYPES	35	1353.3743	12.06	****
ERROR	70	112.1918		
COEFF. OF VAR. = 0.29 STD. ERROR = 6.12 STD. DEVIATION = 10.59				

8. WING AREA

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	20.1987	0.71	NS
GENOTYPES	35	39.6588	1.39	NS
ERROR	70	28.4627		
COEFF. OF VAR. = 0.47 STD. ERROR = 3.08				
STD. DEVIATION = 5.34				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	203.4761	3.00	NS
GENOTYPES	35	163.2511	2.41	***
ERROR	70	67.7156		
COEFF. OF VAR. = 0.23				
STD. DEVIATION = 8.23 STD. ERROR = 4.75				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	83.6477	0.87	NS
GENOTYPES	35	311.7357	3.23	****
ERROR	70	96.3784		
COEFF. OF VAR. = 0.23				
STD. DEVIATION = 9.82 STD. ERROR = 5.67				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	98.4380	1.09	NS
GENOTYPES	35	244.6569	2.72	****
ERROR	70	89.9783		
COEFF. OF VAR. = 0.21				
STD. DEVIATION = 0.49 STD. ERROR = 5.48				

9. AURICLE AREA

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	37.6465	3.75	*
GENOTYPES	35	71.2620	7.09	****
ERROR	70	10.0450		
COEFF. OF VAR. = 1.01 STD. ERROR = 1.83 STD. DEVIATION = 3.17				

2nd Leaf (reanalysed data)

SOURCE	DF	MS	F	SIG.
BLOCKS	2	17.2737	1.82	NS
GENOTYPES	27	83.4766	8.78	****
ERROR	54	9.5079		
COEFF. OF VAR. = 0.88 STD. ERROR = 1.78 STD. DEVIATION = 3.08				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	60.1567	3.86	*
GENOTYPES	35	281.2295	18.06	****
ERROR	70	15.5757		
COEFF. OF VAR. = 0.09 STD. DEVIATION = 3.95 STD. ERROR = 2.28				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	145.6197	7.85	***
GENOTYPES	35	446.4760	24.08	****
ERROR	70	18.5440		
COEFF. OF VAR. = 0.09 STD. ERROR = 2.49 STD. DEVIATION = 4.31				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	59.1364	3.27	*
GENOTYPES	35	371.7644	20.58	****
ERROR	70	18.0683		
COEFF. OF VAR. = 0.086 STD. ERROR = 2.454 STD. DEVIATION = 4.251				

10. VEIN ANGLE

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	3.8084	0.29	NS
GENOTYPES	35	199.6095	15.39	****
ERROR	70	12.9711		
COEFF. OF VAR. = 0.11 STD. ERROR = 2.08				
STD. DEVIATION = 3.60				

2nd Leaf (reanalysed data)

SOURCE	DF	MS	F	SIG.
BLOCKS	2	1.9677	0.19	NS
GENOTYPES	27	121.0576	11.46	****
ERROR	54	10.5658		
COEFF. OF VAR. = 0.10 STD. ERROR = 1.88				
STD. DEVIATION = 3.25				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	5.9051	0.22	NS
GENOTYPES	35	348.9249	13.14	****
ERROR	70	26.5614		
COEFF. OF VAR. = 0.43 STD. DEVIATION = 5.15 STD. ERROR = 2.98				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	12.5423	0.90	NS
GENOTYPES	35	252.0942	18.02	****
ERROR	70	13.9894		
COEFF. OF VAR. = 0.38 STD. ERROR = 2.16 STD. DEVIATION = 3.74				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	2.4033	0.23	NS
GENOTYPES	35	132.4624	12.72	****
ERROR	70	10.4121		
COEFF. OF VAR. = 0.44 STD. ERROR = 1.86 STD. DEVIATION = 3.23				

11. LEAF DRY WEIGHT

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.0021	0.07	NS
GENOTYPES	35	0.1352	4.41	****
ERROR	70	0.0306		
COEFF. OF VAR. = 0.34 STD. ERROR = 0.10				
STD. DEVIATION = 0.18				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.0802	0.49	NS
GENOTYPES	35	0.5933	3.60	****
ERROR	70	0.1648		
COEFF. OF VAR. = 0.23				
STD. DEVIATION = 0.41 STD. ERROR = 0.23				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.0369	0.18	NS
GENOTYPES	35	1.0833	5.35	****
ERROR	70	0.2525		
COEFF. OF VAR. = 0.23				
STD. DEVIATION = 0.45 STD. ERROR = 0.26				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	0.3368	2.25	NS
GENOTYPES	35	0.3822	2.55	****
ERROR	70	0.1496		
COEFF. OF VAR. = 0.19				
STD. DEVIATION = 0.39 STD. ERROR = 0.22				

12. LEAF AREA

(a) 2nd Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	2141.0093	0.71	NS
GENOTYPES	35	8949.5450	3.21	****
ERROR	70	2789.3997		
COEFF. OF VAR. = 0.42 STD. ERROR = 30.49				
STD. DEVIATION = 52.81				

(b) 7th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	13288.3982	1.34	NS
GENOTYPES	35	46039.9069	4.65	****
ERROR	70	9900.3029		
COEFF. OF VAR. = 0.24 STD. ERROR = 57.45				
STD. DEVIATION = 99.50				

(c) 12th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	4036.8611	0.31	NS
GENOTYPES	35	110730.6357	8.37	****
ERROR	70	13225.0040		
COEFF. OF VAR. = 0.19 STD. ERROR = 66.40				
STD. DEVIATION = 115.0				

(d) 17th Leaf

SOURCE	DF	MS	F	SIG.
BLOCKS	2	28680.5278	1.83	NS
GENOTYPES	35	59017.0929	3.76	****
ERROR	70	15694.3944		
COEFF. OF VAR. = 0.18 STD. ERROR = 72.33				
STD. DEVIATION = 125.28				

APPENDIX 5
GENOTYPIC MEAN FOR 8 x 8 ORIGINAL DATA

1. LEAF RATIO

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	3.72	2.12	2.18	1.84
21	2.65	2.01	1.85	1.65
22	1.85	1.59	1.68	1.54
31	2.70	2.12	2.01	2.06
32	2.00	1.77	1.86	1.71
33	1.67	1.70	1.84	1.75
41	5.06	2.72	2.40	2.09
42	3.01	2.52	1.87	1.99
43	3.33	2.48	2.24	2.19
44	5.33	2.78	2.50	2.36
51	8.29	4.34	2.89	2.44
52	5.71	3.68	3.16	2.62
53	5.32	3.17	2.78	2.35
54	7.43	3.40	3.16	2.55
55	7.32	4.49	3.55	2.92
61	5.18	3.54	3.26	2.45
62	4.51	3.28	2.59	2.31
63	5.45	3.45	2.74	2.24
64	7.38	5.41	3.68	3.11
65	11.50	6.36	5.11	4.33
66	5.58	4.77	3.94	3.83
71	6.11	3.04	2.61	2.37
72	3.57	2.86	2.51	2.28
73	3.74	2.51	2.34	2.15
74	4.34	3.05	2.32	2.18
75	6.14	4.62	3.49	2.76
76	7.11	4.79	3.72	3.07
77	6.21	3.13	3.02	2.37
81	5.35	3.11	2.36	2.14
82	4.22	2.87	2.66	2.01
83	4.10	2.83	2.66	2.25
84	4.90	3.23	2.95	2.26
85	12.76	4.88	4.09	3.30
86	12.04	6.02	4.48	3.12
87	6.29	3.30	3.09	2.32
88	6.80	4.25	3.84	2.77
S.E.	0.75	0.31	0.20	0.19
S.E.O.D.	1.06	0.44	0.28	0.26

2. DIFFERENTIAL INDEX

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	3.98	5.02	4.61	5.60
21	5.14	4.24	4.69	4.98
22	5.02	5.35	4.36	5.72
31	5.61	4.76	4.50	3.95
32	6.57	5.07	3.73	3.75
33	8.71	5.81	5.65	6.21
41	3.43	4.42	4.79	5.32
42	7.01	5.30	4.80	4.61
43	4.70	4.76	5.03	3.96
44	3.70	4.99	5.09	5.40
51	1.85	3.40	3.96	4.97
52	2.81	2.61	4.06	4.38
53	2.10	3.47	3.16	4.29
54	3.69	3.72	3.81	4.97
55	2.86	3.20	3.25	4.68
61	2.45	3.06	2.99	4.43
62	2.71	3.04	3.33	3.81
63	2.86	2.98	4.08	5.07
64	1.87	3.12	2.97	4.80
65	2.93	4.00	4.15	3.15
66	1.73	3.34	2.30	4.39
71	3.32	4.14	4.92	5.08
72	6.22	4.55	3.82	3.51
73	4.62	4.16	4.22	4.44
74	4.22	3.92	5.48	5.70
75	2.38	2.67	3.92	4.71
76	2.26	2.48	3.50	4.52
77	2.90	3.31	4.85	4.66
81	2.74	4.50	4.09	6.00
82	3.75	3.50	3.26	4.59
83	3.37	3.64	3.73	4.63
84	3.73	3.20	3.86	4.39
85	1.44	3.76	3.28	4.15
86	2.18	2.75	3.38	3.96
87	2.24	2.93	4.04	4.14
88	2.53	2.39	3.15	4.45
S.E.	0.66	0.47	0.43	0.50
S.E.O.D.	0.93	0.67	0.61	0.71

3. RAPER'S INDEX I

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	2.84	2.24	2.17	2.11
21	2.54	2.37	2.19	2.18
22	2.68	2.78	2.44	2.22
31	2.49	2.29	2.23	2.16
32	2.46	2.30	2.31	2.14
33	2.16	2.28	2.20	2.00
41	2.39	2.18	1.92	2.06
42	2.43	2.22	2.34	2.12
43	2.48	2.42	2.28	2.31
44	2.43	2.01	2.07	1.97
51	2.50	2.04	1.94	2.02
52	2.34	2.13	2.04	2.12
53	2.22	2.04	1.98	1.95
54	2.69	2.35	1.98	1.95
55	2.45	1.89	1.89	2.22
61	2.68	2.31	2.18	2.04
62	2.28	2.01	2.14	2.18
63	2.62	1.97	2.18	2.18
64	2.67	2.90	1.85	1.70
65	2.57	1.87	1.97	1.97
66	3.13	3.79	1.74	1.76
71	2.75	2.12	2.16	2.14
72	2.35	2.28	2.25	2.21
73	2.49	2.12	2.17	2.12
74	2.35	2.05	1.94	1.96
75	2.57	2.16	2.09	2.06
76	2.91	2.01	2.27	1.92
77	2.50	1.84	2.02	2.14
81	2.03	1.98	1.95	1.98
82	2.22	2.11	2.03	2.13
83	2.80	1.99	1.95	2.01
84	2.22	1.84	1.88	1.96
85	2.17	1.79	1.78	1.79
86	2.43	2.00	1.78	1.99
87	2.23	1.70	1.82	2.05
88	1.86	1.66	1.67	1.81
S.E.	0.19	0.20	0.10	0.09
S.E.O.D.	0.27	0.29	0.14	0.13

4. RAPER'S INDEX II

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	2.42	3.19	4.56	5.48
21	1.77	2.64	3.32	3.68
22	1.83	2.55	2.86	2.81
31	1.60	2.31	3.58	3.89
32	2.05	2.61	2.62	3.26
33	2.02	2.63	3.05	3.16
41	2.44	2.45	3.59	6.06
42	2.13	1.81	3.13	4.16
43	1.61	1.87	2.56	3.58
44	5.74	2.56	3.53	4.89
51	2.17	2.32	4.62	5.81
52	2.88	2.53	2.11	3.06
53	2.21	2.04	2.83	4.29
54	4.93	6.79	2.16	4.27
55	7.42	6.56	3.77	2.43
61	2.72	3.63	4.17	5.59
62	4.54	1.72	3.18	2.90
63	4.36	1.99	2.77	4.07
64	5.43	10.14	3.76	4.28
65	3.59	6.91	6.63	10.40
66	6.63	9.39	10.75	9.49
71	3.13	2.40	4.87	6.33
72	1.68	1.96	2.46	3.95
73	1.88	2.27	2.93	3.85
74	3.36	2.29	3.57	5.25
75	5.92	3.05	4.27	4.86
76	6.05	6.58	3.44	4.96
77	2.69	3.35	4.69	6.20
81	6.57	2.73	4.54	5.07
82	2.45	1.96	2.91	3.90
83	1.57	2.20	2.92	4.43
84	5.76	2.84	3.26	3.85
85	5.69	6.66	5.21	3.79
86	5.69	6.34	7.13	7.57
87	7.03	3.50	4.65	4.29
88	6.91	5.57	3.87	4.00
S.E.	0.66	0.83	0.72	0.55
S.E.O.D.	0.94	1.17	1.03	0.78

5. TIP SCORE

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	3.72	3.00	3.00	2.84
21	3.00	2.51	2.45	2.28
22	2.67	1.84	2.06	2.28
31	3.00	2.67	2.51	2.51
32	2.28	2.28	2.06	1.84
33	1.84	1.84	1.84	1.84
41	3.72	3.33	3.22	3.00
42	3.17	3.00	2.84	2.51
43	3.50	2.84	2.84	2.67
44	3.50	3.17	3.00	2.67
51	4.16	3.72	3.33	3.17
52	4.16	3.50	3.72	3.39
53	3.94	3.33	3.33	3.00
54	4.16	3.72	3.72	3.33
55	4.16	3.72	4.16	3.94
61	3.33	3.17	3.55	3.33
62	3.72	3.33	3.17	3.17
63	3.94	3.50	3.33	3.00
64	4.16	3.72	3.72	3.72
65	4.16	4.16	4.16	4.16
66	4.16	4.16	4.16	3.50
71	3.94	3.33	3.50	3.33
72	3.17	3.17	3.17	3.00
73	3.50	3.00	3.00	3.17
74	3.72	3.33	3.17	2.84
75	4.16	4.16	3.94	3.50
76	4.16	4.16	3.94	3.17
77	3.94	3.33	3.50	3.33
81	3.94	3.17	3.33	3.00
82	3.50	3.00	3.00	2.67
83	3.50	2.84	3.00	2.84
84	3.94	3.33	3.00	2.84
85	4.16	3.94	3.94	3.50
86	4.16	4.16	3.94	3.55
87	3.94	3.55	3.50	3.17
88	4.16	3.50	3.33	3.17
S.E	0.14	0.14	0.18	0.18
S.E.O.D.	0.20	0.20	0.26	0.26

6. PETIOLE LENGTH (mm)

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	21.0	54.3	82.3	75.6
21	20.0	36.3	62.6	71.6
22	9.3	17.0	41.3	58.0
31	22.6	41.3	60.3	68.6
32	12.0	24.3	35.0	52.0
33	10.6	28.6	42.0	45.3
41	32.0	60.3	105.0	100.6
42	19.6	44.0	68.6	90.6
43	17.3	51.6	62.0	81.3
44	33.0	69.6	109.0	121.0
51	37.6	63.6	107.0	124.6
52	22.6	67.3	95.0	112.0
53	27.6	88.0	109.3	117.6
54	29.3	66.3	106.0	133.6
55	70.3	124.3	125.0	124.3
61	105.0	69.3	97.3	101.6
62	32.0	60.6	96.6	96.6
63	35.6	81.3	103.3	88.0
64	59.3	76.3	100.0	129.3
65	62.3	92.0	120.6	120.6
66	82.3	91.6	163.0	114.6
71	28.6	67.0	98.6	108.6
72	23.3	58.6	70.6	91.6
73	27.6	67.3	87.3	84.3
74	22.0	52.0	90.3	119.3
75	33.0	73.6	100.3	121.0
76	37.6	87.0	117.3	141.3
77	28.6	78.3	94.3	109.0
81	48.3	80.3	110.6	101.6
82	32.3	61.6	102.6	87.6
83	38.3	84.0	108.6	108.3
84	41.6	86.3	131.0	112.0
85	76.0	99.6	140.6	126.3
86	82.6	126.3	145.6	143.6
87	50.0	87.6	128.3	126.3
88	99.6	126.0	138.3	136.0
S.E.	14.1	6.9	7.8	8.9
S.E.O.D.	20.0	9.8	11.1	12.7

7. WING WIDTH (mm)

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	36.7	41.3	34.7	45.7
21	52.7	59.3	80.3	75.3
22	68.3	100.0	102.3	90.0
31	58.3	57.7	54.3	56.7
32	65.3	81.7	100.0	89.3
33	69.0	91.7	87.7	82.7
41	26.7	37.3	21.3	31.0
42	33.0	49.0	46.3	43.3
43	42.3	55.7	50.7	40.7
44	9.7	51.0	30.0	21.3
51	23.0	44.7	22.0	20.0
52	27.3	40.7	39.7	39.7
53	29.7	42.3	27.0	32.0
54	7.7	18.7	33.0	17.3
55	8.3	14.0	30.3	49.7
61	35.3	40.3	26.7	31.0
62	19.0	45.7	42.0	56.0
63	15.7	43.3	32.7	41.0
64	8.3	10.0	24.7	14.7
65	8.3	12.0	14.0	11.7
66	9.0	11.7	14.7	15.3
71	20.0	45.7	16.7	24.0
72	30.3	48.7	41.0	41.0
73	35.3	41.3	37.7	36.3
74	21.3	41.7	21.0	19.0
75	11.0	19.3	18.3	19.3
76	9.0	18.7	31.3	17.7
77	18.0	32.3	17.3	19.7
81	11.3	30.3	26.0	32.0
82	30.7	48.7	46.3	58.3
83	47.0	39.3	36.0	38.0
84	15.3	36.0	20.0	38.7
85	5.3	12.7	12.3	21.3
86	7.3	12.7	15.0	13.3
87	8.3	31.7	18.7	27.0
88	9.3	18.7	14.3	26.3
S.E.	5.8	4.5	6.3	6.1
S.E.O.D.	8.2	6.3	8.9	8.6

8. WING AREA (cm³)

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	13.50	27.61	34.68	40.08
21	15.26	27.68	43.96	54.76
22	15.03	22.78	50.65	54.94
31	16.02	31.08	41.11	45.36
32	11.16	25.02	42.23	51.25
33	9.60	32.44	39.74	44.52
41	13.79	30.58	34.87	38.24
42	10.28	30.73	42.86	49.70
43	13.07	40.93	38.32	40.12
44	10.10	41.89	47.06	37.03
51	8.68	26.06	27.87	38.76
52	10.01	46.10	51.23	49.38
53	11.33	51.21	50.53	50.09
54	3.90	42.24	52.39	36.40
55	11.77	40.92	42.93	77.06
61	13.03	33.31	37.13	36.93
62	13.75	39.03	61.88	64.56
63	14.29	44.93	59.99	46.26
64	17.35	49.52	36.68	39.90
65	10.20	33.15	41.02	44.57
66	5.49	20.65	69.50	49.51
71	9.48	35.41	28.78	33.82
72	9.75	34.58	41.17	47.91
73	10.13	39.04	42.33	41.54
74	7.08	28.61	29.60	36.02
75	9.36	43.61	30.06	36.44
76	8.27	40.09	50.13	38.77
77	7.37	33.81	27.69	34.28
81	12.23	35.19	43.65	46.53
82	12.03	39.36	60.33	51.21
83	22.16	42.03	52.47	54.43
84	10.22	42.06	49.53	54.47
85	7.06	28.47	29.45	42.19
86	11.37	36.05	36.41	46.66
87	9.11	36.58	39.78	52.79
88	17.80	33.87	46.82	52.61
S.E.	3.09	4.75	5.67	5.47
S.E.O.D.	4.36	6.72	8.02	7.75

9. AURICLE AREA (cm^3)

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	3.7	15.0	8.9	7.2
21	7.8	19.5	17.2	12.9
22	17.3	39.3	30.5	24.6
31	9.6	25.0	18.2	12.5
32	14.4	32.0	31.0	21.6
33	15.8	27.3	19.1	14.9
41	4.6	9.5	6.9	4.7
42	1.3	21.2	21.0	12.3
43	4.5	23.9	23.5	17.5
44	0.0	5.0	8.0	5.2
51	0.0	0.0	3.5	2.5
52	1.1	12.2	11.8	8.7
53	0.0	11.6	12.1	8.0
54	0.0	0.0	5.6	4.5
55	0.0	0.0	0.0	0.0
61	9.4	28.0	0.0	0.0
62	0.0	14.4	14.9	13.7
63	0.0	13.6	14.3	8.1
64	0.0	0.0	0.0	0.0
65	0.0	0.0	0.0	0.0
66	0.0	0.0	0.0	0.0
71	0.8	11.9	5.9	3.0
72	3.7	17.7	20.3	14.8
73	8.6	23.6	19.0	13.8
74	1.9	12.6	14.5	9.1
75	0.0	0.0	0.0	0.0
76	0.0	1.0	0.0	0.0
77	0.0	8.3	3.4	3.2
81	0.0	7.1	3.9	5.2
82	3.4	20.1	15.0	11.4
83	4.6	14.3	15.6	11.9
84	0.0	7.3	4.9	7.9
85	0.0	0.0	0.7	0.9
86	0.0	0.0	0.0	0.0
87	0.0	5.4	1.8	5.4
88	0.0	0.0	0.0	0.0
S.E.	1.8	2.9	2.2	1.9
S.E.O.D.	2.6	4.2	3.1	2.6

10. VEIN ANGLE (degrees)

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	33.9	47.2	55.6	55.0
21	42.8	57.5	69.2	67.5
22	52.2	67.5	73.3	72.2
31	46.4	61.4	64.7	66.4
32	59.7	70.3	75.3	74.5
33	57.2	68.9	74.2	72.5
41	29.7	41.7	42.5	47.2
42	33.9	47.8	55.3	56.9
43	32.5	50.0	56.9	60.3
44	27.7	37.5	40.0	41.4
51	27.8	41.1	39.2	42.2
52	31.4	41.9	39.2	45.8
53	30.6	41.7	44.2	49.7
54	26.9	40.0	37.2	38.3
55	36.1	34.4	35.6	41.7
61	31.9	43.9	44.2	45.8
62	30.0	43.3	46.1	47.5
63	31.4	43.9	49.4	54.2
64	25.8	43.7	39.7	34.7
65	30.8	36.1	33.1	35.3
66	29.7	33.6	35.3	36.1
71	31.9	42.0	42.5	48.9
72	39.7	49.2	53.6	55.8
73	35.3	55.6	60.6	58.3
74	31.7	42.5	43.9	45.6
75	30.6	41.1	36.7	42.5
76	32.5	36.4	37.8	39.7
77	29.2	40.3	41.9	43.5
81	30.0	40.6	46.9	46.7
82	32.2	45.3	54.2	55.6
83	35.0	45.3	49.7	56.9
84	27.2	38.3	38.1	47.5
85	30.8	38.1	37.2	37.5
86	26.7	36.9	33.9	36.4
87	28.3	36.9	39.2	47.5
88	28.6	30.6	34.2	36.9
S.E.	2.1	2.3	2.5	2.5
S.E.O.D.	2.9	3.2	3.5	3.5

11. LEAF DRY WEIGHT (g)

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	0.68	2.21	2.20	2.03
21	0.74	2.37	2.45	2.34
22	0.45	2.36	2.94	2.09
31	0.63	2.18	2.42	2.41
32	1.31	2.47	3.04	2.48
33	0.88	2.16	3.29	2.30
41	0.39	1.62	2.01	2.03
42	0.48	2.25	2.94	2.25
43	0.50	2.25	2.49	2.38
44	0.36	1.91	1.81	1.82
51	0.45	1.50	1.38	1.51
52	0.49	1.68	2.02	2.36
53	0.50	1.62	2.08	2.01
54	0.19	1.41	1.46	1.97
55	0.38	1.28	1.00	1.77
61	0.55	1.60	1.89	1.85
62	0.65	2.20	3.32	3.13
63	0.50	1.85	2.17	2.66
64	0.46	1.68	1.51	1.66
65	0.25	1.06	1.09	1.73
66	0.43	1.09	1.61	2.04
71	0.47	1.81	1.90	1.79
72	0.44	2.32	2.05	2.12
73	0.36	2.38	2.44	2.26
74	0.37	1.69	2.13	2.21
75	0.30	1.28	1.40	1.65
76	0.41	1.43	1.77	1.67
77	0.34	1.87	1.85	2.38
81	0.65	1.60	1.59	1.69
82	0.71	1.98	2.08	2.09
83	0.84	1.51	2.04	2.12
84	0.42	1.58	1.83	2.31
85	0.21	0.95	1.09	1.44
86	0.35	0.94	1.19	1.77
87	0.55	1.65	1.69	2.04
88	0.59	1.12	1.47	1.53
S.E.	0.10	0.23	0.26	0.22
S.E.O.D.	0.14	0.33	0.37	0.32

12. LEAF AREA (cm³)

GENOTYPES	2nd leaf	7th leaf	12th leaf	17th leaf
11	220	615	769	760
21	176	573	845	927
22	231	698	1158	848
31	201	527	772	913
32	274	655	939	955
33	204	588	1024	870
41	92	397	552	774
42	99	412	711	824
43	99	424	657	750
44	110	364	557	600
51	112	354	475	603
52	89	333	523	687
53	138	491	658	742
54	52	303	499	602
55	102	345	410	639
61	128	421	516	681
62	152	499	855	895
63	111	444	669	800
64	114	351	523	573
65	62	189	270	408
66	122	274	504	585
71	101	390	580	687
72	85	407	621	808
73	77	549	689	698
74	76	384	530	695
75	72	277	442	522
76	108	288	422	455
77	67	333	466	748
81	152	397	642	664
82	147	492	746	829
83	214	430	634	813
84	98	384	539	755
85	51	208	359	471
86	71	200	326	554
87	116	378	548	711
88	143	293	440	505
S.E.	31	57	66	72
S.E.O.D.	43	81	94	102

APPENDIX 6

ESTIMATES OF Vr (ARRAY VARIANCE), Wr (ARRAY PARENT-OFFSPRING COVARIANCE), (Wr + Vr) AND (Wr - Vr) FOR BOTH THE 8 x 8 ORIGINAL DATA AND 7 x 7 REANALYSED DATA

1. LEAF RATIO

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	4.5493	4.3289	8.8782	-0.2204
2	1.8781	2.6511	4.5293	0.7730
3	2.0092	2.6373	4.6465	0.6280
4	3.6365	2.6765	6.3130	-0.9600
5	11.2208	3.6089	14.8297	-7.6120
6	11.0651	4.1498	15.2149	-6.9153
7	2.4505	2.0674	4.5180	-0.3831
8	12.1468	4.7176	16.8644	-7.4292
b) 7th leaf				
1	0.7685	0.9609	1.7293	0.1924
2	0.5916	0.9039	1.4955	0.3123
3	0.4164	0.7898	1.2063	0.3735
4	1.4074	0.9616	2.3690	-0.4458
5	1.1857	1.0496	2.2354	-0.1360
6	1.9977	1.2749	3.2725	-0.7228
7	0.7942	0.9127	1.7068	0.1185
8	1.4484	1.3447	2.7931	-0.1037
c) 12th leaf				
1	0.2921	0.3361	0.6282	0.0439
2	0.3186	0.4305	0.7491	0.1119
3	0.1757	0.3441	0.5198	0.1684
4	0.3677	0.4756	0.8433	0.1078
5	0.7189	0.5476	1.2665	-0.1713
6	0.7869	0.6446	1.4314	-0.1423
7	0.3216	0.4465	0.7681	0.1248
8	0.7751	0.6508	1.4259	-0.1243
d) 17th leaf				
1	0.1261	0.1960	0.3221	0.0699
2	0.1726	0.2366	0.4092	0.0641
3	0.0757	0.1331	0.2089	0.0574
4	0.1980	0.2562	0.4542	0.0582
5	0.5224	0.4263	0.9486	-0.0960
6	0.6639	0.4666	1.1305	-0.1973
7	0.1399	0.2050	0.3449	0.0651
8	0.3425	0.3359	0.6784	-0.0066

2. DIFFERENTIAL INDEX

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	2.0809	2.5165	4.5974	0.4357
2	4.4049	3.1729	7.5778	-1.2320
3	5.3843	4.8196	10.2039	-0.5646
4	3.1304	1.7544	4.8848	-1.3760
5	1.3557	0.0652	1.4209	-1.2905
6	0.3819	0.3588	0.7407	-0.0231
7	2.8289	2.5166	5.3455	-0.3123
8	0.8727	1.0710	1.9436	0.1984
b) 7th leaf				
1	0.7619	0.4625	1.2244	-0.2994
2	1.4244	0.9665	2.3909	-0.4579
3	1.3297	1.0887	2.4184	-0.2410
4	1.1507	1.0280	2.1787	-0.1228
5	1.1953	-0.0572	1.1382	-1.2525
6	0.5653	0.0217	0.5869	-0.5436
7	0.9598	0.8684	1.8282	-0.0914
8	1.0638	0.5840	1.6478	-0.4798
c) 12th leaf				
1	0.7283	0.7015	1.4298	-0.0268
2	0.4011	0.3840	0.7851	-0.0171
3	1.4430	1.2224	2.6654	-0.2206
4	0.8026	1.0431	1.8457	0.2406
5	0.4413	-0.0817	0.3596	-0.5229
6	0.6839	0.1678	0.8517	-0.5161
7	0.7735	0.3500	1.1236	-0.4235
8	0.5518	0.3608	0.9126	-0.1910
d) 17th leaf				
1	0.8630	0.0191	0.8821	-0.8439
2	0.7524	0.1749	0.9274	-0.5775
3	1.4895	0.4246	1.9130	-1.0639
4	1.0061	0.0333	1.0394	-0.9727
5	0.6007	0.2038	0.8045	-0.3969
6	0.9064	0.1701	1.0765	-0.7362
7	0.8076	0.0669	0.8745	-0.7406
8	0.7593	0.4762	1.2355	-0.2832

3. RAPER'S INDEX I

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	0.0842	0.0892	0.1735	0.0050
2	0.0561	0.0283	0.0844	-0.0278
3	0.1637	0.0015	0.1652	-0.1622
4	0.0677	0.0637	0.1314	-0.0039
5	0.0988	0.0815	0.1803	-0.0173
6	0.1842	0.0833	0.2675	-0.1010
7	0.1396	0.1019	0.2415	-0.0377
8	0.1549	0.0170	0.1719	-0.1378
b) 7th leaf				
1	0.0426	0.0841	0.1266	0.0415
2	0.0734	0.0224	0.0957	-0.0510
3	0.0584	-0.0203	0.0380	-0.0787
4	0.3195	0.0967	0.4162	-0.2227
5	0.0553	-0.0264	0.0290	-0.0818
6	0.7620	0.4200	1.1820	-0.3420
7	0.0456	0.0588	0.1044	0.0132
8	0.0404	0.0802	0.1205	0.0398
c) 12th leaf				
1	0.0328	0.0148	0.0476	-0.0180
2	0.0334	0.0355	0.0689	0.0021
3	0.0341	0.0316	0.0657	-0.0024
4	0.0478	0.0411	0.0889	-0.0068
5	0.0231	0.0196	0.0427	-0.0035
6	0.0772	0.0366	0.1138	-0.0405
7	0.0619	0.0150	0.0770	-0.0469
8	0.0282	0.0340	0.0621	0.0058
d) 17th leaf				
1	0.0280	0.0089	0.0370	-0.0191
2	0.0251	0.0003	0.0254	-0.0248
3	0.0301	0.0024	0.0325	-0.0277
4	0.0460	0.0187	0.0648	-0.0273
5	0.0356	0.0264	0.0620	-0.0092
6	0.0434	0.0101	0.0535	-0.0333
7	0.0213	0.0102	0.0315	-0.0111
8	0.0235	0.0029	0.0264	-0.0206

4. RAPER'S INDEX II

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	3.3661	1.7612	5.1273	-1.6049
2	1.3698	1.5135	2.8833	0.1437
3	1.2083	0.6613	1.8696	-0.5470
4	4.3879	3.7918	8.1797	-0.5960
5	4.5985	3.5193	8.1178	-1.0792
6	2.9279	1.0751	4.0030	-1.8527
7	5.4502	4.6404	10.0906	-0.8098
8	5.6161	2.4343	8.0504	-3.1819
b) 7th leaf				
1	0.4652	0.5393	1.0045	0.0741
2	0.6599	-0.3111	0.3487	-0.9710
3	0.1801	-0.4203	-0.2402	-0.6004
4	10.2386	8.1251	18.3637	-2.1135
5	10.4065	5.5810	15.9874	-4.8254
6	13.8691	4.0623	17.9314	-9.8068
7	3.1355	2.8136	5.9491	-0.3219
8	10.3026	9.0242	19.3268	-1.2784
c) 12th leaf				
1	1.0122	-0.1214	0.8908	-1.1336
2	0.4452	0.3027	0.7479	-0.1424
3	0.2222	0.0619	0.2841	-0.1603
4	0.6627	0.5487	1.2114	-0.1140
5	3.6014	3.8036	7.4050	0.2022
6	10.2480	6.5150	16.7630	-3.7330
7	1.2283	0.3473	1.5757	-0.8810
8	4.3730	4.5909	8.9639	0.2179
d) 17th leaf				
1	1.8265	1.0708	2.8974	-0.7557
2	0.4977	0.0395	0.5372	-0.4583
3	0.4279	0.3138	0.7417	-0.1141
4	1.3800	0.8980	2.2780	-0.4821
5	7.1483	5.4225	12.5708	-1.7257
6	8.2901	1.8875	10.1776	-6.4025
7	1.3820	1.1873	2.5693	-0.1947
8	2.1022	2.7768	4.8791	0.6746

5. TIP SCORE

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	0.1793	0.2428	0.4221	0.0635
2	0.3444	0.3875	0.7319	0.0431
3	0.5947	0.5543	1.1489	-0.0404
4	0.0847	0.1272	0.2119	0.0425
5	0.0063	0.0301	0.0365	0.0238
6	0.0562	0.0362	0.0924	-0.0199
7	0.0908	0.1617	0.2525	0.0710
8	0.0353	0.1155	0.1508	0.0803
b) 7th leaf				
1	0.2089	0.2780	0.4869	0.0690
2	0.3765	0.4412	0.8177	0.0647
3	0.3497	0.4305	0.7803	0.0808
4	0.1288	0.2394	0.3682	0.1105
5	0.0628	0.1283	0.1912	0.0656
6	0.1100	0.1697	0.2797	0.0598
7	0.1504	0.2351	0.3856	0.0846
8	0.1881	0.3073	0.4954	0.1192
c) 12th leaf				
1	0.2895	0.3270	0.6165	0.0376
2	0.4108	0.4600	0.8708	0.0492
3	0.3690	0.4393	0.8083	0.0704
4	0.1992	0.2248	0.4241	0.0255
5	0.0847	0.1343	0.2190	0.0496
6	0.1057	0.2021	0.3078	0.0964
7	0.1168	0.2163	0.3330	0.0996
8	0.1472	0.2543	0.4015	0.1071
d) 17th leaf				
1	0.2260	0.2448	0.4707	0.0189
2	0.3799	0.3384	0.7183	-0.0414
3	0.2970	0.3123	0.6093	0.0153
4	0.2105	0.2271	0.4375	0.0167
5	0.1612	0.1987	0.3599	0.0375
6	0.1618	0.1153	0.2771	-0.0465
7	0.1278	0.1039	0.2318	-0.0239
8	0.1999	0.2072	0.4071	0.0073

6. PETIOLE LENGTH

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	1955.4167	703.4524	2658.8691	-1251.9643
2	101.7857	235.1310	336.9167	133.3452
3	152.9881	322.6012	475.5893	169.6131
4	268.1369	417.5714	685.7083	149.4345
5	757.4583	859.4107	1616.8690	101.9524
6	2111.4107	391.4821	2502.8929	-1719.9286
7	158.5655	190.4464	349.0119	31.8810
8	802.8274	820.8750	1623.7024	18.0476
b) 7th leaf				
1	277.8691	564.3333	842.2024	286.4643
2	393.7024	737.2143	1130.9167	343.5119
3	734.4881	995.3571	1729.8452	260.8690
4	250.9167	449.4048	700.3214	198.4881
5	624.0417	569.2262	1193.2679	-54.8155
6	507.3571	672.2143	1179.5714	164.8571
7	321.8750	366.8214	688.6964	44.9464
8	600.0595	751.0238	1351.0833	150.9643
c) 12th leaf				
1	554.2976	778.2738	1332.5714	223.9762
2	750.8452	1072.1369	1822.9822	321.2917
3	1027.3453	1216.1072	2243.4524	188.7619
4	610.6547	770.5000	1381.1548	159.8452
5	340.6190	468.5119	809.1309	127.8929
6	751.7024	910.4702	1662.1726	158.7679
7	429.3691	702.1310	1131.5000	272.7619
8	374.3215	721.8452	1096.1667	347.5238
d) 17th leaf				
1	530.5595	653.6310	1184.1905	123.0714
2	526.4941	686.4167	1212.9107	159.9226
3	785.4702	837.5774	1623.0476	52.1071
4	444.4405	568.0536	1012.4940	123.6131
5	295.3750	126.1250	421.5000	-169.2500
6	609.7024	636.8452	1246.5476	27.1428
7	392.0297	502.1071	894.1369	110.0774
8	549.8690	547.5179	1097.3869	-2.3512

7. WING WIDTH

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	361.0000	403.8572	764.8571	42.8571
2	474.7143	550.1190	1024.8333	75.4048
3	386.7738	428.3333	815.1071	41.5595
4	242.8036	344.0298	586.8333	101.2262
5	133.2738	278.4643	411.7381	145.1905
6	119.1905	103.4762	222.6667	-15.7143
7	160.6310	226.4762	387.1072	65.8452
8	229.3333	332.7857	562.1190	103.4524
b) 7th leaf				
1	127.2976	272.1786	399.4762	144.8809
2	477.8869	670.9405	1148.8274	193.0535
3	434.4940	654.1667	1088.6607	219.6726
4	303.8690	461.1190	764.9881	157.2500
5	275.7321	338.0119	613.7440	62.2798
6	281.6607	449.7619	731.4226	168.1012
7	138.9881	211.9405	350.9286	72.9524
8	189.9643	418.6428	608.6071	228.6786

c) 12th leaf

1	596.0119	683.7083	1279.7202	87.6964
2	904.0357	898.8036	1802.8393	-5.2321
3	746.3452	884.8512	1631.1964	138.5060
4	175.6845	388.3631	564.0476	212.6786
5	223.1190	300.5476	523.6667	77.4286
6	154.7797	274.2798	429.0595	119.5000
7	132.9167	275.9822	408.8988	143.0655
8	167.3095	389.8215	557.1310	222.5119

12th leaf (parent 1 deleted)

2	899.3810	1074.6667	1974.0476	175.2857
3	860.8254	1036.4444	1897.2698	175.6191
4	187.2857	440.5317	627.8175	253.2460
5	221.3809	348.1429	569.5238	126.7619
6	162.1429	310.1349	472.2778	147.9922
7	135.1429	307.7063	442.8492	172.5635
8	176.2698	446.1032	622.3730	269.8333

d) 17th leaf

1	504.7083	513.9524	1018.6607	9.2440
2	548.4226	486.6905	1035.1131	-61.7321
3	540.0833	586.9226	1127.0060	46.8393
4	158.7381	246.9881	405.7262	88.2500
5	262.4583	314.4047	576.8631	51.9464
6	306.3452	394.0357	700.3810	87.6905
7	92.3453	224.8095	317.1548	132.4643
8	230.8750	331.7559	562.6309	100.8810

8. WING AREA

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	20.8992	6.0670	26.9661	-14.8321
2	21.3099	0.1655	21.4755	-21.1444
3	50.5287	21.1159	71.6446	-29.4127
4	36.2812	1.8847	38.1659	-34.3964
5	32.2606	0.0867	32.3473	-32.1739
6	28.0703	5.7997	33.8700	-22.2707
7	19.4454	-6.0157	13.4297	-25.4610
8	39.1643	6.0487	45.2129	-33.1156
b) 7th leaf				
1	63.5167	-19.4820	44.0347	-82.9987
2	86.2697	5.9961	92.2657	-80.2736
3	103.6351	16.8247	120.4598	-86.8104
4	91.2430	11.8769	103.1199	-79.3662
5	153.7063	-6.5704	147.1359	-160.2766
6	133.7915	45.8889	179.6804	-87.9027
7	78.1187	18.1138	96.2325	-60.0047
8	52.8172	10.8329	63.6501	-41.9843
c) 12th leaf				
1	113.2655	10.1535	123.4190	-103.1121
2	118.1061	78.0638	196.1699	-40.0422
3	129.2815	91.3460	220.6274	-37.9355
4	102.0612	7.3918	109.4530	-94.6693
5	214.2127	92.2139	306.4266	-121.9988
6	233.1765	107.7650	340.9415	-125.4114
7	99.0008	70.5299	169.5308	-28.4709
8	175.8126	3.7490	179.5617	-172.0636
d) 17th leaf				
1	84.4899	18.7574	103.2473	-65.7326
2	114.8608	23.1836	138.0444	-91.6772
3	54.1081	43.3071	97.4153	-10.8010
4	134.2465	1.1311	135.3776	-133.1154
5	238.8787	191.7619	430.6406	-47.1167
6	124.5177	40.8395	165.3572	-83.6782
7	66.7797	38.0103	104.7900	-28.7695
8	144.7938	-17.3548	127.4389	-162.1487

9. AURICLE AREA

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	24.5604	16.0065	40.5669	-8.5539
2	55.5808	56.2438	111.8246	0.6630
3	47.5723	40.1106	87.6829	-7.4618
4	9.6754	6.2156	15.8910	-3.4598
5	0.5075	3.6416	4.1492	3.1341
6	11.0989	-1.2608	9.8381	-12.3596
7	17.3745	23.6384	41.0129	6.2638
8	4.4404	13.4540	17.8944	9.0136
2nd leaf (parent 7 deleted)				
1	25.9637	15.5212	41.4849	-10.4425
2	63.2648	63.7843	127.0491	0.5195
3	46.6420	49.7824	96.4244	3.1405
4	11.1359	7.4293	18.5653	-3.7066
5	0.5800	4.0678	4.6478	3.4878
6	12.6844	-2.4935	10.1909	-15.1779
8	4.9688	14.9041	19.8729	9.9353

b) 7th leaf

1	102.1407	60.2956	162.4363	-41.8451
2	116.2637	121.7473	238.0110	5.4836
3	92.0826	99.6280	191.7106	7.5455
4	97.5363	118.8295	216.3658	21.2932
5	33.0890	76.1955	109.2846	43.1065
6	129.9175	97.5848	227.5023	-32.3327
7	85.7250	95.2858	181.0108	9.5608
8	60.3021	106.7941	167.0962	46.4920

c) 12th leaf

1	52.8684	67.1991	120.0676	14.3307
2	60.7339	70.2694	131.0033	9.5356
3	53.4509	62.4116	115.8625	8.9608
4	87.4585	68.8516	156.3101	-18.6069
5	31.0165	51.6123	82.6288	20.5958
6	50.9937	64.7599	115.7537	13.7662
7	86.4822	84.7872	171.2693	-1.6950
8	43.7288	65.1457	108.8745	21.4169

d) 17th leaf

1	28.0995	35.5646	63.6641	7.4651
2	39.4786	42.6106	82.0093	3.1320
3	36.1938	40.6959	76.8897	4.5022
4	38.4172	29.3212	67.7384	-9.0959
5	16.5623	31.5587	48.1210	14.9963
6	28.8188	44.4490	73.2677	15.6302
7	43.1868	46.1270	89.3138	2.9402
8	24.8554	36.1516	61.0070	11.2962

10. VEIN ANGLE

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	52.2973	70.0591	122.3565	17.7618
2	132.7740	110.4870	243.2610	-22.2871
3	149.9509	121.6056	271.5565	-28.3453
4	15.0677	24.5864	39.6542	9.5187
5	15.6715	8.9308	24.6022	-6.7407
6	8.2312	8.0877	16.3189	-0.1435
7	28.4041	36.4863	64.8904	8.0822
8	16.2279	32.6432	48.8711	16.4154
2nd leaf(parent 2 deleted)				
1	45.4971	57.8345	103.3316	12.3374
3	100.5389	88.7475	189.2864	-11.7913
4	13.4416	15.1556	29.0372	2.1539
5	17.7298	7.7399	25.4697	-9.9899
6	9.5203	8.8430	18.3633	-0.6772
7	16.7776	19.4165	36.1941	2.6389
8	17.4917	31.0719	48.5635	13.5802

b) 7th leaf

1	82.6414	116.2974	198.9388	33.6560
2	127.7331	164.8161	292.5492	37.0829
3	133.5036	162.6356	296.1391	29.1320
4	34.8114	58.8949	93.7063	24.0834
5	17.3338	30.9383	48.2722	13.6045
6	30.5147	40.4479	70.9626	9.9333
7	51.4298	86.1987	137.6285	34.7688
8	28.9203	61.7884	90.7087	32.8682

c) 12th leaf

1	147.2095	178.5577	325.7671	31.3482
2	186.2717	204.4034	390.6751	18.1317
3	147.8925	188.4395	336.3320	40.5471
4	72.5418	125.1184	197.6602	52.5767
5	16.6971	43.0750	59.7721	26.3778
6	56.3763	93.8615	150.2378	37.4851
7	80.6734	132.9920	213.6653	52.3186
8	65.1279	124.6343	189.7623	59.5064

d) 17th leaf

1	112.6768	141.8417	254.5186	29.1649
2	127.8850	143.9921	271.8772	16.1071
3	97.9994	124.8863	222.8857	26.8869
4	79.9351	115.4694	195.4045	35.5343
5	29.8414	65.0007	94.8421	35.1594
6	60.9652	105.7388	166.7040	44.7736
7	58.5415	93.0139	151.5554	34.4724
8	74.2981	115.1178	189.4159	40.8197

11. LEAF DRY WEIGHT

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	0.0468	0.0242	0.0710	-0.0226
2	0.1194	0.0416	0.1610	-0.0778
3	0.1320	0.0363	0.1683	-0.0957
4	0.0249	0.0175	0.0423	-0.0074
5	0.0243	0.0130	0.0373	-0.0112
6	0.0226	-0.0002	0.0224	-0.0227
7	0.0225	-0.0033	0.0193	-0.0257
8	0.0561	0.0333	0.0895	-0.0228
b) 7th leaf				
1	0.2173	0.1276	0.3449	-0.0897
2	0.2390	0.1499	0.3888	-0.0891
3	0.3268	0.1554	0.4822	-0.1714
4	0.2914	0.1629	0.4542	-0.1285
5	0.1010	0.1530	0.2540	0.0520
6	0.2497	0.1917	0.4414	-0.0580
7	0.1946	0.1676	0.3622	-0.0270
8	0.1841	0.1999	0.3840	0.0158
c) 12th leaf				
1	0.2414	0.2895	0.5308	0.0482
2	0.5218	0.2997	0.8214	-0.2221
3	0.4058	0.3983	0.8042	-0.0075
4	0.3029	0.3775	0.6804	0.0746
5	0.2572	0.2789	0.5361	0.0218
6	0.6774	0.4079	1.0852	-0.2695
7	0.2417	0.2299	0.4717	-0.0117
8	0.1874	0.2517	0.4391	0.0642
d) 17th leaf				
1	0.1469	0.0894	0.2363	-0.0575
2	0.3233	0.0503	0.3737	-0.2730
3	0.1112	0.0533	0.1646	-0.0579
4	0.1382	0.0354	0.1737	-0.1028
5	0.1916	0.0079	0.1995	-0.1838
6	0.4118	0.0858	0.4976	-0.3260
7	0.1679	0.0873	0.2552	-0.0806
8	0.1821	0.0442	0.2262	-0.1379

12. LEAF AREA

ARRAY	Vr	Wr	Wr + Vr	Wr - Vr
a) 2nd leaf				
1	7203.8214	6125.9524	13329.7738	-1077.8691
2	7106.7798	4262.6726	11369.4524	-2844.1071
3	6273.9821	4621.0655	10895.0476	-1652.9167
4	1119.8214	931.3095	2051.1309	-188.5119
5	1466.5357	982.3333	2448.8691	-484.2024
6	1708.0357	-150.3452	1557.6905	-1858.3810
7	808.4940	119.8572	928.3512	-688.6369
8	3253.2262	2837.3274	6090.5536	-415.8988
b) 7th leaf				
1	14380.2559	12236.8095	26617.0655	-2143.4464
2	32445.3036	18872.2619	51317.5655	-13573.0417
3	19598.5655	17180.1726	36778.7381	-2418.3929
4	6671.3929	1995.8095	8667.2024	-4675.5834
5	11756.9405	11619.2797	23376.2202	-137.6607
6	18051.6310	15202.2083	33253.8393	-2849.4226
7	10940.5417	4254.4940	15195.0357	-6686.0476
8	12649.2738	13274.9405	25924.2143	625.6667
c) 12th leaf				
1	25656.8691	34358.7560	60015.6250	8701.8869
2	53621.5000	57053.2024	110674.7024	3431.7024
3	32405.3274	43818.3214	76223.6488	11412.9940
4	11156.2500	19991.4345	31147.6845	8835.1845
5	23712.0179	23945.6310	47657.6488	233.6131
6	45840.0893	48362.8928	94202.9821	2522.8036
7	17617.6548	21921.4047	39539.0595	4303.7500
8	26156.8928	35182.2798	61339.1726	9025.3869
d) 17th leaf				
1	23234.1072	14728.2083	37962.3155	-8505.8988
2	14601.4405	5260.8095	19862.2500	-9340.6310
3	22602.1607	9182.1964	31784.3571	-13419.9643
4	18451.7083	7128.0774	25579.7857	-11323.6310
5	23037.3036	13160.7381	36198.0417	-9876.5655
6	32402.5416	14973.0000	47375.5417	-17429.5417
7	24534.3690	9739.1310	34273.5000	-14795.2381
8	30723.5833	18045.4822	48769.0655	-12678.1012

APPENDIX 7

ESTIMATES OF THE SECOND DEGREE STATISTICS FOR
BOTH THE 8 x 8 ORIGINAL DATA AND 7 x 7 REANALYSED
DATA (IN BRACKETS)

CHARACTER	Vp	$\bar{W}_r$	$\bar{V}_r$	$V\bar{r}$	E
1. LEAF RATIO					
a) 2nd leaf	5.6298	3.3547	6.1195	2.9900	1.6849
b) 7th leaf	1.6408	1.0248	1.0762	0.6572	0.2917
c) 12th leaf	0.8695	0.4845	0.4696	0.3105	0.1030
d) 17th leaf	0.6021	0.2820	0.2801	0.1457	0.1030
2. DIFFERENTIAL INDEX					
a) 2nd leaf	6.8419	2.0344	2.5550	0.9704	1.3023
b) 7th leaf	1.7747	0.6203	1.0564	0.2475	0.6725
c) 12th leaf	1.9064	0.5185	0.7282	0.1729	0.5662
d) 17th leaf	1.0764	0.1961	0.8980	0.0664	0.7569
3. RAPER'S INDEX I					
a) 2nd leaf	0.2365	0.0583	0.1187	0.0139	0.1086
b) 7th leaf	0.5688	0.0894	0.1746	0.0242	0.1239
c) 12th leaf	0.0759	0.0285	0.0423	0.0130	0.0280
d) 17th leaf	0.0466	0.0100	0.0316	0.0051	0.0248
4. RAPER'S INDEX II					
a) 2nd leaf	6.1431	2.4240	3.6156	1.2760	1.3238
b) 7th leaf	8.9430	3.6768	6.1572	1.9810	2.0461
c) 12th leaf	7.7078	2.0061	2.7241	0.6530	1.5765
d) 17th leaf	5.7683	1.6995	2.8818	0.6922	0.9214
5. TIP SCORE					
a) 2nd leaf	0.6128	0.2069	0.1740	0.0824	0.0613
b) 7th leaf	0.6609	0.2789	0.1969	0.1251	0.0600
c) 12th leaf	0.6470	0.2823	0.2154	0.1313	0.9920
d) 17th leaf	0.5016	0.2185	0.2205	0.1088	0.1013
6. PETIOLE LENGTH					
a) 2nd leaf	1425.75	492.62	788.57	228.36	600.56
b) 7th leaf	1741.64	638.20	463.79	270.09	145.11
c) 12th leaf	1975.37	829.99	604.89	375.92	183.60
d) 17th leaf	1324.89	569.78	516.74	274.46	241.31

CHARACTER	V_p	$\overline{W_r}$	$\overline{V_r}$	$\overline{V_r}$	E
7. WING WIDTH					
a)					
b) 7th leaf	1215.98	434.60	278.74	170.62	60.21
c) 12th leaf	1255.44	512.04	387.53	217.73	118.48
	(1448.19)	(566.25)	(377.49)	(226.22)	(84.71)
d) 17th leaf	966.08	387.44	330.50	189.40	112.19
8. WING AREA					
a) 2nd leaf	40.08	4.39	31.00	3.04	28.46
b) 7th leaf	108.85	10.44	95.39	7.94	67.72
c) 12th leaf	223.01	57.65	148.11	26.34	96.38
d) 17th leaf	234.55	42.46	120.33	19.66	89.98
9. AURICLE AREA					
a) 2nd leaf	69.56	19.76	21.35	6.96	10.05
	(76.17)	(21.86)	(23.61)	(8.09)	(9.51)
b) 7th leaf	218.15	97.05	89.63	48.16	26.50
c) 12th leaf	127.34	66.89	58.34	41.72	13.99
d) 17th leaf	83.54	38.31	31.95	20.62	10.41
10. VEIN ANGLE					
a) 2nd leaf	140.91	51.61	52.33	22.13	12.97
	(118.82)	(32.75)	(31.57)	(10.67)	(10.57)
b) 7th leaf	233.88	90.25	63.36	36.34	15.58
c) 12th leaf	288.99	136.39	96.60	67.20	18.54
d) 17th leaf	235.46	113.13	80.27	58.92	10.07
11. LEAF DRY WEIGHT					
a) 2nd leaf	0.0633	0.0203	0.0561	0.0163	0.0306
b) 7th leaf	0.4340	0.1635	0.2255	0.0955	0.1648
c) 12th leaf	0.7547	0.3167	0.3545	0.1588	0.2025
d) 17th leaf	0.2073	0.0567	0.2091	0.0391	0.1496
12. LEAF AREA					
a) 2nd leaf	9067	2466	3617	1042	2789
b) 7th leaf	38089	11829	15811	6288	9900
c) 12th leaf	91069	35579	29520	14983	13225
d) 17th leaf	29977	11527	23698	8615	15694