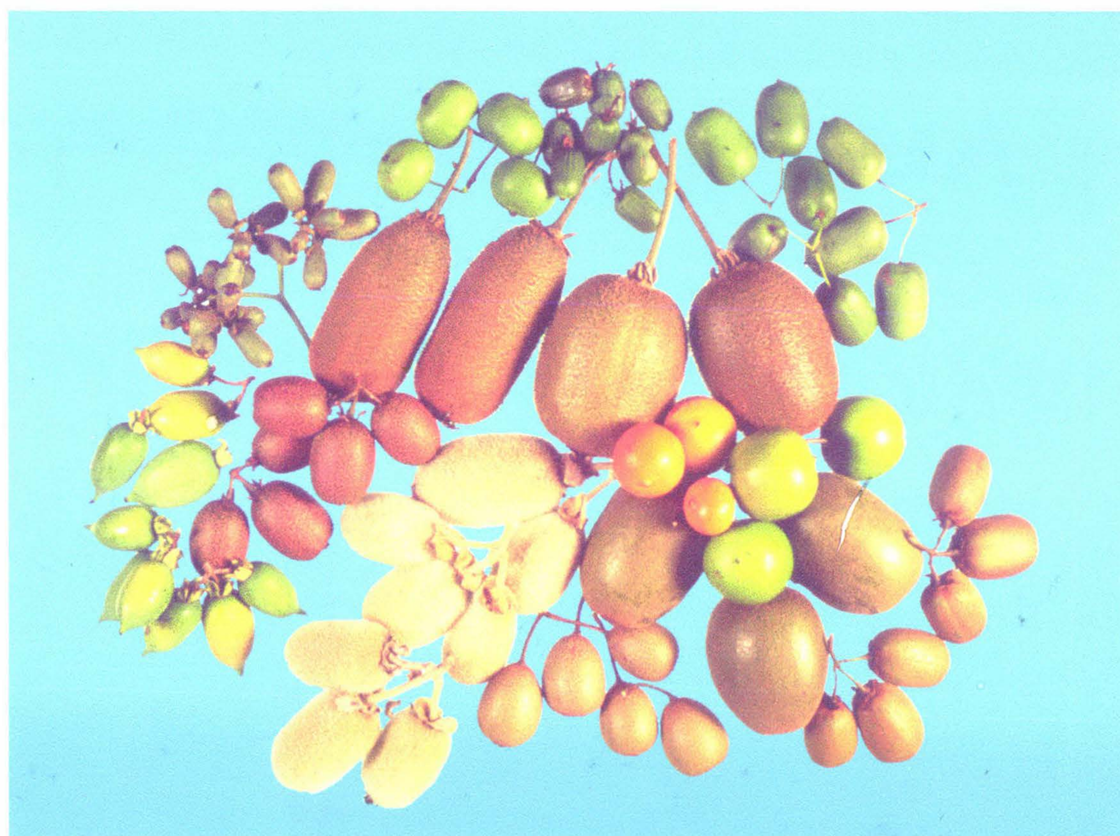
Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

Phenotypic Variation of Kiwifruit in a Factorial Mating Design

(***Actinidia deliciosa*** (A.CHEV.) C.F. LIANG *et* A.R. FERGUSON **var. deliciosa**)



A thesis presented in partial fulfilment of the requirements for the degree of Master of Applied Science at Massey University

Hinga Marsh

1999

Abstract

Systematic evaluation of the New Zealand *A.deliciosa* var. *deliciosa* breeding population was conducted using a two-factor factorial mating design (FMD). Two separate populations were used to study the genetic properties of the New Zealand *A.deliciosa* germplasm. Crosses were made in spring 1991, between seven female and seven male parents, resulting in one population [referred to as *Factorial One*] and another population resulting from six female and seven male parents [referred to as *Factorial Two*]. These ninety-one biparental families each had thirty-six seedlings planted during spring 1992 in a randomised complete block (RCB) design. Trunk diameters on all seedlings (at 20 cm above ground level) were measured annually from 1993 to 1996. Flowering characters were measured from both male and female seedlings in spring 1995. The sexual maturity of these populations had reached 68 %, with a female to male ratio of 1:1.32 by the 1995 flowering season. From these sexually mature seedlings, almost six hundred females were assessed for various fruiting characters of interest during the 1996 fruit season. Significance tests for vegetative and fruiting characters were reported based on their '*female*' (main effect), '*male*' (main effect) and '*female* by *male*' (interaction effect). Results from these statistics showed significant genetic variation exists for many of the vegetative, floral and fruiting characters measured within the two reference populations. Narrow sense (additive) heritabilities of ≥ 0.4 were reported in 11 of the 29 characters from Factorial One and 14 of the 29 characters in Factorial Two. The high additive genetic variation, present in both reference populations, indicates reasonable genetic advances are possible for at least some of these characters. Fruit weight and fruit shape characters in both factorial sets were highly heritable, while fruit quality aspects such as taste, flavour and texture generally had low heritabilities. Genetic and phenotypic correlations were also estimated for some selected vegetative and fruiting characters. These results showed distinct differences (as well as similarities) existed between the two reference populations. Genetic correlations r_a of $\geq |0.7|$ were reported, in 8 and 9 of the 30 (selected) vegetative correlations in Factorials One and Two respectively. From the 34 (selected) fruiting correlations in Factorials One and Two there were 17 and 7 genetic correlations $\geq |0.7|$ respectively. When comparing the same r_a correlations, between both Factorial data sets, it was evident that at least some of correlations could be in opposite directions to each other. General combining abilities (GCA), based on family means, were calculated and significant differences were evident amongst these means for several characters from both female and male classifiers of their half sib arrays. In addition, male (paternal) lines were equally as potent when compared to female (maternal) lines for their effects on their female offspring's fruiting characters. Therefore it is important to identify male parents breeding value (viz. progeny tests) for various characters, in order to improve the response to selection, because only half the genetic gain is possible when selecting one parent (female) as opposed to applying selection pressure to both parents (male and female). The ability to apply selection pressure to both parents, for a single character, could possibly lead to twice the genetic gain.

Acknowledgments

Ki taku whaiaipo ki a Edith me ta maua tamahine me Te Maringi mai o Hawaiiki Aneta mo to raua arohamai tautokomai i a matou te whanau i nga wa katoa.

He mihi aroha ki toku koroua ki a Rarunga Wihapi i moe atu i te arohatanga o ona matua tupuna me tana moe wahine a Mariao Wihapi, ko raua nei aaku wakaruruhau, na raua nei ahau i whakatipu ake i kiia ai he tangata.

Ki toku kaiako maraurau ko Takuta Ian Gordon no te Wharewananga o Manawatu tenei te mihi atu ki a ia. Nana nei i timata ahau ki whai i te matauranga o te putaiao i nga hua rakau

He mihi ano hoki ki a koutou nga kaimahi i awhina mai nei i ahau i te otinga o tenei mahi tino uaua.

Noreira tena koutou tena koutou tena no tatou katoa.

To my wife Edith and our daughter Te Maringi mai o Hawaiiki Aneta for sharing their love and support throughout our lives together.

To my late grandfather Rarunga Wihapi and his wife Mariao Wihapi, a very special thanks for their love and care which has grown me into the person I am.

To the learned Dr Ian Gordon of Massey University, for whom I must especially thank, for starting this my journey of learning about the science of plant breeding.

And to all those people, who have helped in every way to allow me to complete this manuscript, I thank you all very sincerely.

TABLE OF CONTENTS

ABSTRACT ii

ACKNOWLEDGMENTS iii

I. INTRODUCTION 1

A. NEW ZEALAND KIWIFRUIT 1
B. FACTORIAL MATING DESIGN (FMD) 2
1. VEGETATIVE CHARACTERISTICS 3
2. FRUITING CHARACTERISTICS 4
C. BIOLOGY OF A.DELICIOSA - KIWIFRUIT 5
D. PRODUCTION OF KIWIFRUIT 6
1. NEW CULTIVARS IN KIWIFRUIT BREEDING 8

II. LITERATURE REVIEW 10

A. PLANT BREEDING IN KIWIFRUIT 10
1. LIMITATIONS IN PERENNIAL PLANT BREEDING 11
2. JUVENILE PERIOD IN PERENNIAL FRUIT CROPS 13
B. QUANTITATIVE GENETICS IN A FACTORIAL MATING DESIGN 19
1. PHENOTYPIC VARIATION OF METRIC TRAITS 19
a) Phenotypic and environmental deviations 20
b) Population mean (M) 20
c) Breeding value (A) and average allele concept 21
2. VARIANCE COMPONENTS AND QUANTITATIVE TRAITS 23
3. FACTORIAL MATING DESIGN 26
4. COVARIANCE OF RELATIVES 28
C. HERITABILITY ESTIMATES AND THEIR PRECISION 31
1. GENETIC VARIATION AND PREDICTED RESPONSE 33
2. PRECISION OF HERITABILITY ESTIMATES 34
a) Estimation of a variance component 35
b) Standard error of the variance 36
c) Variance of a heritability (ratio of mean squares) 37
D. GENERAL AND SPECIFIC COMBINING ABILITIES 39
1. COMBINING ABILITY AND MEAN PERFORMANCE 39
a) GCA estimation from family means 40
2. COMBINING ABILITY AND VARIANCE ANALYSIS 41
E. PHENOTYPIC AND GENETIC CORRELATIONS 42
1. PHENOTYPIC (SIMPLE) CORRELATIONS 42
2. GENOTYPIC CORRELATIONS OF VEGETATIVE CHARACTERS 44
F. SELECTION STRATEGIES FOR IMPROVEMENT 47
1. MASS (PHENOTYPIC) SELECTION 48
2. FAMILY SELECTION 48
a) Sib selection 49
b) Progeny testing 49
3. WITHIN FAMILY SELECTION 50
4. COMPARING RESPONSE TO SELECTION STRATEGIES 50

III. MATERIALS AND METHODS 51

A. EXPERIMENTAL DESIGN 52
1. STATISTICAL DESIGN AND ANALYSES 54
a) Inference Base of the Factorial Mating Design Study 54
B. PROBLEM OF DATA IMBALANCE 58
1. REDUCED FMD APPROACH FOR VEGETATIVE DATA 59
2. REDUCED FMD APPROACH FOR FRUITING DATA 59

III. MATERIALS AND METHODS
a) Sex at flowering – male or female 59
b) Female plants distributions 60
c) Optimum plot size for female distribution 61
3. ADVANTAGES OF THE REDUCED FMD APPROACH 64
4. LIMITATIONS OF USING REDUCED FMD 64
C. VEGETATIVE AND FRUITING CHARACTERS 65
1. PLANT CHARACTERISTICS 65
2. FRUITING CHARACTERISTICS 67
D. ANOVA OF VEGETATIVE AND FRUITING CHARACTERS 74
1. SIGNIFICANCE TESTING OF VARIANCE COMPONENTS 77
2. EXPECTATIONS OF MEAN SQUARES FOR VEGETATIVE CHARACTERS 77
3. EXAMPLE OF VARIANCE COMPONENT ESTIMATION 79
4. ESTIMATING THE WITHIN PLOT GENETIC VARIANCE 81
E. GENETICAL ESTIMATES OF CHARACTERS 82
1. HERITABILITY ESTIMATES 82
2. GCA MEAN AND VARIANCE BASED ESTIMATES 83
a) Significance testing of GCA (means) 83
b) Significance testing of SCA (means) 84
c) Significance testing of GCA/SCA (variance) 85
F. SUMMARY 86
IV. RESULTS AND DISCUSSION 87
A. VEGETATIVE DATA RESULTS 87
1. SEXUAL MATURITY AND SEX RATIOS 90
2. GLM - ANOVA OF VEGETATIVE DATA 92
a) Combining abilities GCA_{var} and SCA_{var} 92
b) Expectations of mean squares for vegetative characters 94
3. VARIANCE COMPONENT ESTIMATION 95
4. GENETICAL ESTIMATES OF VEGETATIVE CHARACTERS 96
a) Heritability estimates 96
b) Combining abilities GCA_{mean} and SCA_{mean} 98
5. PHENOTYPIC CORRELATIONS OF VEGETATIVE CHARACTERS 101
6. GENOTYPIC CORRELATIONS OF VEGETATIVE CHARACTERS 104
B. FRUITING DATA RESULTS 109
1. FRUIT CHARACTERISTICS 109
2. GLM - ANOVA OF FRUITING DATA 112
a) Combining abilities GCA_{var} and SCA_{var} 112
3. GENETICAL ESTIMATES OF FRUIT CHARACTERS 115
a) Heritability estimates 115
b) Combining abilities GCA_{mean} and SCA_{mean} 119
4. PHENOTYPIC CORRELATIONS OF FRUITING CHARACTERS 123
5. GENOTYPIC CORRELATIONS OF FRUITING CHARACTERS 129
C. DISCUSSION OF RESULTS 133
D. CONCLUSIONS AND RECOMMENDATIONS 145
1. CONCLUSIONS 145
2. RECOMMENDATIONS 147
V. APPENDICES 148
1. APPENDIX A : LIST OF REFERENCE TABLES 148
2. APPENDIX B: EXPERIMENTAL DESIGN AND LAYOUT 154
BIBLIOGRAPHY 157

LIST OF TABLES

Table II-1 : Relative merits to plant breeding of various features amongst long-lived perennials. 12
Table II-2 : Covariances and genetical variances of relatives (from Becker 1992). 30
Table III-1 : Summary of parental arrays and full sib families in Factorial One 52
Table III-2 : Summary of parental arrays and full sib families in Factorial Two 53
Table III-3 :Probability of a specified number of female (or male) vines flowering in a plot; also their expected and observed plot totals (with the specified genders) in each class. 61
Table III-4 : Expected plot numbers of a binomial distribution having specific female (or male) classes and a plot size of nine. 62
Table III-5 : Expected mean squares for a randomised complete block, factorial mating design in a single environment [infinite random] (from Hallauer and Miranda, 1981). 75
Table IV-1 : Population statistics for ten vegetative characters in Factorial One 5x5 and Factorial Two 6x6 designs. 88
Table IV-2 : Trends in the differences between the means of ten vegetative characters across Factorial One (5x5) and Factorial Two (6x6). 89
Table IV-3 : Summary of 1995 sex ratios for all maternal arrays in Factorial One and Two. 91
Table IV-4 : Estimated mean squares of ten vegetative characters and their F-test significance. 92
Table IV-5 : Estimates of the partitioned variance component and their t-test significance from zero. 95
Table IV-6 : Heritability estimates and approximate standard errors for ten vegetative characters in Factorial One and Two. 97
Table IV-7 : Estimates of GCA_{mean} effects by parental arrays as deviations from the population mean in 5 selected vegetative characters from Factorial One 99
Table IV-8 : Estimates of GCA_{mean} effects by parental arrays as deviations from the population mean in 5 selected vegetative characters from Factorial Two. 99
Table IV-9 : Phenotypic simple correlations in ten vegetative characters and their significance from zero from Factorial One (5x5) design and Factorial (6x6) design. 102
Table IV-10 : Summary of simple phenotypic correlations in ten vegetative characters (r>0.20). 103
Table IV-11 : Genetic [*g*] (±SE) and phenotypic [*p*] (significance from zero) correlations estimated in ten vegetative characters in Factorial One (5x5) design. 105
Table IV-12 : Genetic [*g*] (±SE) and phenotypic [*p*] (significance from zero) estimated in ten vegetative characters in Factorial Two (6x6) design. 106
Table IV-13 : Trends in the differences between genetic & phenotypic correlations of Factorial One (3x7) and Factorial Two (3x4) designs. 107
Table IV-14 : Population statistics for nineteen fruiting characters in Factorial One (3x7) reduced design. 109
Table IV-15 : Population statistics for nineteen fruiting characters in Factorial Two (3x4) reduced design. 110
Table IV-16 : Trends in the differences between means of nineteen fruiting attributes in Factorial One (3x7) and Factorial One (3x4) reduced designs. 111
Table IV-17 : Estimated mean squares of nineteen fruit characters and their F-test significance from Factorial One (3x7) design. 112
Table IV-18 : Expected mean squares of nineteen fruit characters and their F-test significance from Factorial Two (3x4) design. 113
Table IV-19 : Narrow sense heritability estimates and their approximate standard errors for nineteen fruiting characters in Factorials One (3x7) and Two (3x4) designs. 117
Table IV-20 : Dominance heritability estimates and their approximate standard errors for nineteen fruiting characters in Factorials One (3x7) and Two (3x4) designs. 118

LIST OF TABLES

Table IV-21 : Estimates of GCA_{mean} effects by female parental arrays as deviations from the population mean in 19 selected fruit characters from Factorial One 3x7. 119

Table IV-22 : Estimates of GCA_{mean} effects by male parental arrays as deviations from the population mean in 19 selected fruit characters from Factorial One 3x7. 120

Table IV-23 : Estimates of GCA_{mean} effects by female parental arrays as deviations from the population mean in 19 selected fruit characters from Factorial Two 3x4. 121

Table IV-24 : Estimates of GCA_{mean} effects by male parental arrays as deviations from the population mean in 19 selected fruit characters from Factorial Two 3x4. 122

Table IV-25 : Summary of simple phenotypic correlations in nineteen fruiting characters in Factorial One (3x7) design and Factorial Two (3x4) design. 124

Table IV-26 : Summary of simple phenotypic correlations in nineteen fruiting characters in Factorial One (3x7) design. 125

Table IV-27 : Summary of simple phenotypic correlations in nineteen fruiting characters in Factorial Two (3x4) design.. 126

Table IV-28 : Summary of simple phenotypic correlations in nineteen fruiting characters in Factorial One (3x7) design and Factorial Two (3x4) design. 127

Table IV-29 : Summary of differences between certain simple phenotypic correlations in fruiting characters (r>0.20 in at least one case). 128

Table IV-30 : Summary of genetic [**g**] (±SE) and phenotypic [**p**] correlations estimated nineteen fruiting characters in Factorial One (3x7) design. 130

Table IV-31 : Summary of Genetic [**g**] (±SE) and phenotypic [**p**] correlations estimated nineteen fruiting characters in Factorial Two (3x4) design. 131

Table IV-32 : Trends in the genetic & phenotypic correlations between fruiting characters from Factorial One 3x7 and Factorial Two 3x4. 132

Table V-1 : Factorial One and Two gender flowering summaries for 1995, 1996 detailed by block and sub-total by factorial. 148

Table V-2 : Factorial One - BiP coding system; and HortResearch accession code identification 149

Table V-3 : Factorial Two - BiP coding system; and HortResearch accession code identification 150

Table V-4: Factorial One - number of plants per plot (1-6), observed and measured for vegetative and fruiting characteristics in 1996. 151

Table V-5 : Factorial Two - number of plants per plot (1-6), observed and measured for vegetative and fruiting characteristics in 1996. 152

LIST OF EQUATIONS

Equation II-1 : Response (R) and generation time (T) in years. 16
Equation II-2 : Phenotypic, genetic (additive & non-additive) and environmental variation 24
Equation II-3 : Estimates of phenotypic covariance of relatives and genetic covariance of relatives as a linear function of their genetic variance components (from Nyquist, 1991). 29
Equation II-4 : Heritability based on an individual plant basis (Hallauer & Miranda, 1981) 32
Equation II-5: Heritability based on entry-mean basis for female (or male) parental array (Hallauer & Miranda, 1981). 32
Equation II-6 : Response (R) or genetic gain. 33
Equation II-7 : Estimate of the standard deviation (or variance) of a variance 36
Equation II-8 : Estimate of the standard error of a variance 36
Equation II-9 : Variance estimate for heritability ratio from Osborne and Paterson (1952) 37
Equation II-10 : Variance estimate for heritability ratio from Dickerson In: Hallauer and Miranda, (1981). 38
Equation II-11 : GCA/SCA means approximation formulae (from Simmonds, 1979). 40
Equation II-12 : Correlation (simple or product moment) coefficient formulae from Steel and Torrie, 1980. 42
Equation II-13 : Phenotypic correlation as a function of genetic and environmental effects. 43
Equation II-14 : Correlated response of an unselected (secondary) character when a primary character is selected for (from Falconer, 1989) 45
Equation II-15 : Relative efficiencies of indirect and direct response between two characters (Falconer, 1989). 46
Equation III-1 :Maturity days to 6.2%SSC; where 6.2%SSC falls within range of %SSC monitored over EBX to LBX. 72
Equation III-2 : Maturity days to 6.2%SSC; where 6.2%SSC falls below the range of %SSC monitored over MBX to LBX. 72
Equation III-3 : Model Statement for FMD single environment experiments (from Hallauer & Miranda, 1981). 76
Equation III-4 : Heritability based on an individual plant basis (Hallauer & Miranda, 1981) 82

LIST OF FIGURES

Figure I-1 : New *A.deliciosa* cultivars 'Tomua' and 'Hayward' 9

Figure II-1 : Flow chart of fast track and conventional plant propagation methods in the New Zealand Plant Breeding programme (NZKBP). 14

Figure IV-1 : Phenotypic and genetic correlations between various floral characters and growth rates in Factorial One (5x5) and Factorial Two (6x6) designs. 133

Figure IV-2 : Phenotypic correlations between various fruiting characters in Factorial One (3x7) and Factorial Two (3x4) designs. 139

Figure IV-3 : Genetic correlations between various fruiting characters in Factorial One (3x7) and Factorial Two (3x4) designs. 140

Figure V-1 : General overview of the external replications layout of FMD design 154

Figure V-2: General design format of the Factorial Mating Design in a randomised complete block. Orchard Blocks 35 & 40 - both have 12 rows (or 4 Blk'd replicates each). Orchard Blocks 46 & 47 - both have 6 rows (or 2 Blk'd replicates). 155

Figure V-3: Pictorial view of the physical layout of each group of six plants/bay/row. 156

Chapter One

Introduction

I. Introduction

A. New Zealand kiwifruit

The kiwifruit is a relatively new commercial crop in comparison to many other fruit tree crops. The fruit is sold on the international fresh fruit market. The prime sensory attributes of kiwifruit include its sweet and acidic flavours (sugar/acid balance), high nutritional value and emerald green flesh (McMath *et al.,* 1991).

The world wide production of kiwifruit is based on the single cultivar, 'Hayward', in the species *Actinidia deliciosa* (A.Chev) C.F. Liang et A.R. Ferguson var. *deliciosa* (*herein referred to as kiwifruit*) (Ferguson and Bollard, 1990). Thus the kiwifruit industry is considered a *monocultural* industry i.e. being based on only one cultivar. The worldwide supply of this cultivar has saturated the international marketplace and eroded the profitability of growing kiwifruit for export in New Zealand. The once lucrative 'Hayward' kiwifruit has now become a marginal fruit crop on the international fruit market (Ferguson *et al.,* 1996).

New Zealand's kiwifruit industry is currently facing much uncertainty, due to the increasing pressure from overseas competitors and the fluctuating market returns. The situation is further exacerbated by the steadily rising cost of production. Therefore it is essential that the kiwifruit industry diversify into new cultivars, allowing New Zealand to reassert its position as the leader in the international kiwifruit market.

The collection of *Actinidia* germplasm and systematic breeding in New Zealand began in the mid-1970's. Since its establishment, in 1992, the Horticulture and Food Research Institute of New Zealand Limited (*herein referred to as HortResearch*) has been charged with responsibility for the New Zealand kiwifruit breeding programme (NZKBP). Consequently the breeding programme itself is very much in its infancy. The main objective of the kiwifruit breeding programme is to increase the probability of selecting a range of superior genotypes for successful commercialisation. The on-going development of new kiwifruit cultivars will depend on the efficacy of the New Zealand kiwifruit breeding programme.

B. Factorial Mating Design (FMD)

The aims of this study were to evaluate the genetic properties of the New Zealand kiwifruit breeding programme *A.deliciosa* germplasm populations as at 1991. This information will increase the scientific knowledge of kiwifruit quantitative genetics. Plant breeding programmes should rely on applied quantitative genetics to develop knowledge about the variation within the plant breeding populations. The information derived by quantitative genetics will allow the plant breeder to make informed decisions about the most efficient selection strategies to employ for achieving the plant breeding objectives. Quantitative genetics provide estimates of various genetical statistics by partitioning the variation into classifiable sources. Several designs such as the diallel, hierarchical and factorial mating designs can be used in order to develop the familial structures necessary for genetical interpretation of the variation. Several issues must be considered when planning the genetic studies of any plant species. These can generally be classified into three broad areas that will help to determine the most appropriate mating design to use, and they are as follows -

- reproductive biology of the plant species
- objectives of the plant breeding programme
- available resources to the programme

The main objective of the New Zealand Kiwifruit Breeding Programmes (NZKBP) was to establish a genetical experiment that would derive information about the significance of utilising controlled crosses (bi-parentals - BiP's) and their effects on several economic fruit traits in kiwifruit. The dioecious nature of kiwifruit makes it difficult to ascertain the breeding value of the male (used as a parent) and its' effects on fruit quality of its female progeny. Consequently, the application of the North Carolina Model II Design i.e. factorial mating design (Comstock and Robinson, 1948), was considered as the most appropriate design, in order to discern these paternal (male) effects. The FMD study is based on a random selection of parents from the New Zealand *A.deliciosa* germplasm.

The inference base population (IBP) is assumed to represent a diverse sampling of the New Zealand *A.deliciosa* population. Selected parents were crossed during November - December 1991 in a factorial mating design (FMD) to produce 91 full sib families. These progenies were planted out in the field, in a randomised complete block design (RCB) in November 1992. Several characters of interest have been measured since. The focus of the factorial mating design (FMD) study for 1996, was the evaluation of fruiting characteristics of 430 female vines across the 91 full sib families. Most of these vines flowered for the first time during November 1995 and the fruit was harvested and assessed during April and May of 1996.

The factorial mating design (FMD) was used in order to estimate genetical statistics about the *A.deliciosa* germplasm currently available in New Zealand. The estimation of these various genetical components and their subsequent use in predicting genetic gain should improve the efficiencies of the New Zealand kiwifruit breeding programme. Future plant breeding decisions concerning the population improvement of *A.deliciosa* germplasm in New Zealand will be enhanced as a result of this FMD study.

1. Vegetative characteristics

Several vegetative characters such as trunk diameter, leaf measurements and flowering attributes (first bloom, mid-bloom and full bloom) have been reported in genetic studies of various perennial fruit crop plants (Hansche *et al.,* 1983; Hansche and Beres 1980; Hayward *et al.,* 1993; Kearsey, 1993). In this study over 3,000 plants were monitored in two RCB factorial designs. Vegetative characters were measured on all individuals in both factorials including trunk diameter, number of prominent (swollen) buds per 500 mm cane, juvenile period, flowering range and median flowering dates.

The objective of both the vegetative and fruiting measurements was to estimate the various genetical statistics pertaining to the 1991 *Actinidia deliciosa* germplasm.

- heritabilities (both narrow and dominance) and their respective standard errors
- general and specific combining ability (GCA/SCA) effects of parental genotypes
- phenotypic and genetic correlations amongst vegetative (and fruiting) characters

The vegetative data could also be used to investigate any significant genetic and/or phenotypic correlations between vegetative and fruiting characters. That is, identifying moderate to high *genetic* correlations between vegetative characters and fruiting characters, that could prove to be very useful as an early (indirect) selection tool for kiwifruit plant breeding. As previously mentioned, the lengthy generation cycle of many perennial fruit tree crops is a major limitation to genetic progress. Therefore, the development of an early selection tool to identify the fruiting potential of seedlings could improve efficiency in perennial fruit breeding programmes. The main reason behind measuring trunk diameters over the four-year period (1993-96) was to investigate if any possible correlation between the early phase (immature) trunk diameters and their floral/fruiting stage i.e. mature phase.

2. Fruiting characteristics

Fruiting characters such as fruit weight, fruit yield (per vine) and post harvest fruit quality characters (sensory, shape descriptors and storage life) are the basis of plant selection in the NZKBP. Fruiting characters were measured on all pistillate (female) vines in Factorial One and Factorial Two, during March to August of 1996, and these data will be referred to, herein, as being from the '1996 fruiting data'. The objective was to determine various genetical statistics relating to these fruiting characteristics accordingly the data were used to estimate the same genetic estimates as for the vegetative characters (listed above). These include heritabilities (both additive and dominance) and their respective standard errors, GCA/SCA effects (general/specific combining abilities) of parental genotypes and phenotypic and genotypic correlations amongst fruiting character.

The main goal of selection in the kiwifruit breeding programme is the development of an improved pistillate selection for commercial release. In order to achieve this, a number of fruiting traits must be monitored, the data analysed appropriately and then individuals selected based on these results. If the primary objective of selecting new commercial cultivars cannot be achieved from the current cycle of F_1 plants, the fruiting data can be analysed for genetic parameters and used to determine the best selection strategy to employ in order to achieve the objective in subsequent cycles (recurrent selection).

C. Biology of A.deliciosa - kiwifruit

All vines in the genus Actinidia have a perennial climbing or scrambling habit. Most species in the genus are deciduous, although there are some evergreen species found in subtropical regions. The genus is mainly confined to China, particularly forested riparian hillsides in central and southern China. Currently, there are some 60 species, most of which have been subdivided so that more than 100 taxa are currently recognised. Of these only two species, *A. deliciosa* and *A. chinensis* are considered commercially important. In general, *A. chinensis* is distributed mainly in the warmer eastern regions of China, while *A. deliciosa* is predominantly found in more western regions (Ferguson *et al.*, 1996). For the purpose of the FMD study, only the *A. deliciosa* will be considered.

The Actinidia genus is assumed to be functionally dioecious, although a genus-wide systematic survey to confirm this has never been conducted. The dioecious condition means male and female flowers are borne on separate vines. These male and female vines are functionally staminate and functionally pistillate vines respectively (McNeilage, 1991). Staminate vines (pollen bearing) have flowers with a rudimentary or undeveloped ovary and have no ovules, however their stamens contain viable pollen. The flowers on the pistillate (egg-bearing) vines have a fully functional ovary containing ovules, but their stamens contain non-viable pollen. These two types of vines are assumed to result from a genetic sex-determining mechanism that is, as yet, poorly understood. There are, at times, deviations from strict dioecism. Fruiting or inconstant males are staminate vines with some flowers capable of fruit set i.e. some flowers with functional ovaries. Conversely, hermaphrodites are morphologically indistinguishable from pistillate vines, but have stamens with viable pollen as well as functional ovaries. Both the fruiting males and hermaphrodite vines are capable of self pollination and fruit set (McNeilage, 1991). These two types of vines occur (naturally) in very low frequencies in the New Zealand *A. deliciosa* germplasm. Therefore female vines from dioecious kiwifruit populations (whose sex is unknown at planting) have an unusual situation with regard to the statistical design and analyses of these fruiting data. The primary concern involves the random distribution of the females (and therefore males) throughout the physical layout of the design leading to possible imbalance in these data (see Chapter Three).

Kiwifruit *A. deliciosa* is a hexaploid with 2n = 6x = 174 and is considered amphidiploid i.e. behaves in a diploid manner with respect to segregating populations (Ferguson *et al.,* 1996; Zhu, 1990; McNeilage and Considine, 1989). This assumption, of amphidipliod behaviour, is crucial for the successful application of genetic theory and variance component analysis for the understanding of polygenic gene action (Hayward and Breese, 1993; Nyquist, 1991; Mayo, 1980; Mettler and Gregg, 1969). There are various polyploid levels across the 60 species within the *Actinidia* genus itself, ranging from diploid through to octaploid types (McNeilage and Considine, 1989). Subsequently, a great deal of natural diversity exists amongst the species within the *Actinidia* genus and high phenotypic variation for many characters has been reported (Beatson, 1991; Zhu, 1990; McNeilage and Considine, 1989).

D. Production of kiwifruit

The first known introduction of kiwifruit into New Zealand, was seed from the Hubei Province, China, in 1904 (*hereafter known as the '1904' introduction*) (Beatson, 1991; Blanchet and Chartier, 1991). Subsequently, the kiwifruit cultivar 'Hayward' was selected from a small seedling population in the mid-1920's by Mr. Hayward Wright; this population is assumed to be one or two generations on from the '1904' introduction. Several other selections were made around the same time i.e. 'Bruno', 'Monty', 'Gracie' and 'Abbott'. However, by the mid-1960's, 'Hayward' had established itself as the preferred commercial cultivar and went on to form the basis of today's kiwifruit industry (Ferguson, 1990). The rapid rise in the popularity of kiwifruit on the international market, saw a dramatic increase in New Zealand kiwifruit planting's between 1970 and 1990. Total planting's in 1994 were estimated at 10,161 ha producing about 70 million trays (225,000 tonnes) of export fruit. More recently, however, the New Zealand production has declined and fluctuates around 50 - 55 million export trays annually (New Zealand Fruit Council, 1995). The other major producers of kiwifruit are Italy, France, Greece, USA, Australia and Chile. These countries collectively produce significant volumes of kiwifruit, with Italy being the largest individual producer. The New Zealand Kiwifruit Marketing Board *(hereafter known as NZKMB)* now has to compete vigorously in the international kiwifruit market.

The oversupply of kiwifruit to the international marketplace has meant diminishing returns for both the local and international growers' alike (Ferguson *et al.,* 1996). The reduced economic viability of many New Zealand orchards has meant some orchardists have been forced out of business. The New Zealand Kiwifruit Marketing Board Limited was established in 1988 to control the export of New Zealand kiwifruit. The NZKMB has sole rights to export kiwifruit to all markets other than Australia (New Zealand Fruit Council, 1995).

Until recently, the common name *kiwifruit* was used by the NZKMB for the international marketing of the fruit, but this has since been supplanted by the generic brand name of '*Zespri*'. The brand name change is an attempt to differentiate the New Zealand kiwifruit, the "world's finest", from the rest of the world kiwifruit production (Kiwifruit Marketing Board, 1997). The increasing pressure from overseas producers has encouraged the NZKMB to look towards new kiwifruit cultivars.

Accordingly, there has been an increase in funding resources given to the HortResearch breeding programme. The relationship between NZKMB and HortResearch is vital to the development of new kiwifruit cultivars to supplement and perhaps even replace the existing single cultivar 'Hayward'. The 'Hayward' cultivar, being a pistillate vine, requires a polleniser (staminate vine) with coincident flowering period in order to achieve fruit set. Currently, a minimum planting ratio of 1:8 male:female is recommended (Sale and Lyford, 1990).

In New Zealand, *A. deliciosa* vines begin flowering in November of each year and their fruit mature in April-May of the following year i.e. some six months after flowering. The 'Hayward' fruit must reach a threshold brix level of 6.2 % soluble solids concentration (%SSC) before being harvested, as measured by refractometer (Beever and Hopkirk, 1990). The average storage life of 'Hayward' fruit can vary from between 6 - 8 months when stored at 0°C and high humidity conditions. The long storage life is one of the prime postharvest attributes of 'Hayward', allowing the fruit to be shipped to international marketplaces. Generally, the fruit arrives in excellent condition for retail distribution and also maintains a good shelf life, which is another important postharvest attribute (McDonald, 1990).

The current planting density for individual kiwifruit vines is 4.8 - 5.0 m within row and 5.5 - 6.0 m between row. This plant density can produce average yields of 25 tonnes/ha and higher. Kiwifruit can be sexually propagated by seed, although these seedlings are not true to type. There are several methods of asexual propagation, which include grafting, softwood or hardwood cuttings, root cuttings and micropropagation (tissue culture). Grafting is the most practicable method of reproducing clones of a cultivar or genotype, for commercial purposes (Lawes, 1990).

Grafting of kiwifruit requires that dormant wood of the cultivar is taken during winter. Scion wood is usually cut into '*two bud scion*' sections. Grafting is best done in early spring, to a suitable seedling rootstock either in a nursery situation or *in-situ* in the field. The most commonly used rootstock for kiwifruit are 'Bruno' seedlings. The relative ease with which kiwifruit can be replicated in this manner facilitates the quick establishment of new cultivars for commercial scale planting's (Lawes, 1990).

1. New cultivars in kiwifruit breeding

Systematic kiwifruit breeding has only been established during the last 10 - 15 years. A major constraint being the long generation cycle of kiwifruit (*3 - 7 years*) from seed raising to the final evaluation cycle (Ferguson *et al.,* 1996). As a consequence, a number of new cultivars are just beginning to be developed. Recent selections from the New Zealand kiwifruit breeding programme (NZKBP) include 'Tomua', a new early maturing cultivar that resulted from *individual selection* from an F_1 population between two accessions of *A. deliciosa* (HortResearch Kiwifruit Breeding, 1996). The cultivar 'Tomua' is very similar to 'Hayward' in many respects but the fruit matures 4-6 weeks earlier than 'Hayward' and has a reduced storage life of 2 - 3 months in comparison to 6 - 8 months for 'Hayward' (Figure I-1). Therefore, 'Tomua' is seen by the Kiwifruit Marketing Board as an 'early niche market' fruit with a possible annual production of 1-2 million trays (Lamb, 1995). Incremental improvements, such as those offered by new cultivar 'Tomua', will not be of medium to long term benefit to the New Zealand industry. Instead, there must be a significant improvement in a suite of characters (several traits) focusing on key attributes considered desirable from both the 'consumer' (taste convenience) and the grower (productivity).

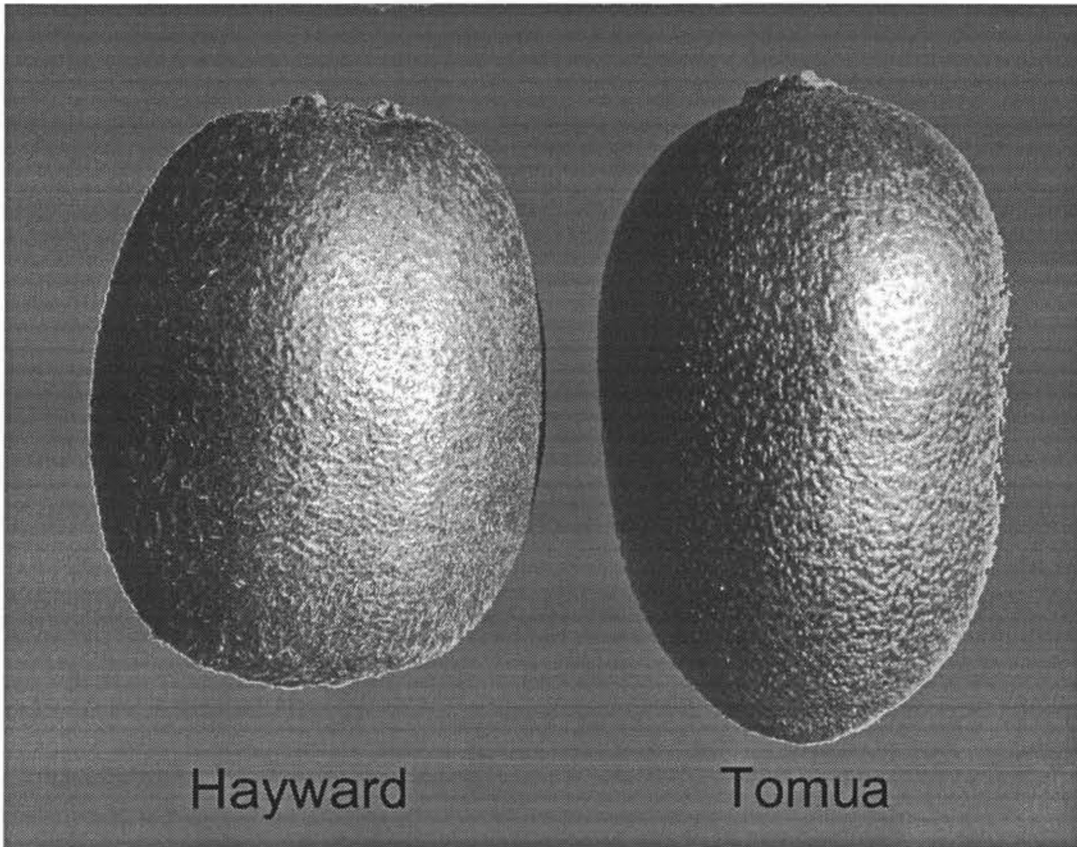


Figure I-1 : New *A.deliciosa* cultivars 'Tomua' and 'Hayward'

Other examples of recently released cultivars include

- ‘MontCap’ - early maturing F_2 seedling from ‘Hayward’ with limited storage life and developed in France (Blanchet, 1995)
- ‘Xuxiang’ – large fruited seedling with higher %SSC soluble solids content than ‘Hayward’ originating from a ‘wild’ population in China (Wei, 1993)
- ‘Miliang 1’ – large fruited seedling with higher %SSC soluble solids content than ‘Hayward’ and originates from another ‘wild’ population in China (Wang, 1995)

In China many of the selections of *A. deliciosa* and *A. chinensis* have being selected straight from the wild and most of these are not readily available outside of China. However in order to challenge the status of ‘Hayward’ these new selections must have substantial improvements in composite (generic) characters such as fruit quality and yield, guaranteeing both a market premium and grower enthusiasm, before they can revolutionise the commercial status of *A. deliciosa*.

II. Literature Review

The study of plant breeding and quantitative genetics in kiwifruit has a relatively short history, with only a few scientific papers published to date (Testolin *et al.,* 1995; Beatson, 1991; Zhu, 1990). In contrast, many scientific papers are available on quantitative genetics of other perennial fruit tree crops such as Malus, Prunus and Pyrus (Hansche, 1986; Janick and Moore, 1983; Visser, 1965). There are many similarities between the traits considered by the Factorial Mating Design (FMD) study and those that have already been examined in other fruit tree crops. Accordingly, the latter results will be used to illustrate plant breeding and quantitative genetics, in the absence of specific kiwifruit examples. These types of parallel comparisons have successfully been made between various other plant species in the literature (Alston and Spielgel-Roy, 1985; Bringhurst, 1983; Visser, 1965).

A. *Plant breeding in kiwifruit*

Plant breeding in *A. deliciosa* is relatively undeveloped when compared to various fruit tree crops. Consequently, there has been very little published on plant breeding in kiwifruit (Zhu, 1990; Beatson, 1991; Testolin *et al.,* 1995; Ferguson *et al.,* 1996). Plant breeding, as defined by Allard (1960) is the "*art and science of changing plants genetically*", with the subsequent increase in "*yield*" being the ultimate aim of the plant breeder. Allard uses "*yield"* in a generic meaning as opposed to the literal biological meaning. There are many examples where quality traits are more important than total biomass i.e. in silviculture breeding where 'clear wood' is one of the main objectives or viticulture breeding where fruit quality is crucial in determining the wine making properties of the grapes. Although, internationally, kiwifruit plant breeding is very much in its infancy there are already several well-defined ideotypes toward which the NZKBP are directed. These ideotypes have been determined, on the basis of characters available or potentially available in HortResearch's *Actinidia* germplasm collection and in collaboration with key market drivers as indicated by the NZKMB. As this information is commercially sensitive the various ideotypes for kiwifruit will not be discussed any further here.

Kiwifruit plant breeding can benefit, I believe, from information already accumulated in other fruit tree crop breeding programmes. Therefore our attention will focus on the limitations to progress in fruit tree crops in general, and its significance to kiwifruit breeding. The NZKBP has, in its first decade of operation, accumulated a large source of *Actinidia* germplasm from a wide range of taxa. Accordingly, there is an increasing awareness of the potential benefits from utilising quantitative plant genetics in the kiwifruit breeding programme. However, careful planning and implementation of genetical experiments such as those by Beatson (1991) and Zhu (1990), together with the current FMD study are necessary in order to develop more quantitative genetic knowledge to aid the New Zealand kiwifruit plant breeding effort.

1. Limitations in perennial plant breeding

Several limitations affecting the progress of plant breeding are common amongst many perennial fruit species. Knight (1966) described progress in plant breeding of apples and pears as "*more of an art than a science*" because "*the impact of modern genetic thought on fruit breeding, in general, has been remarkably slight*". Knights' personal view was that '*modern genetic thought*' needed to be integrated into plant breeding. Twenty years on from Knights 1966 report, Saure (1987) concluded that fruit crop breeding in Europe was still not utilising quantitative genetics because of certain inherent difficulties in perennial fruit breeding. These difficulties include the high cost of maintenance during the juvenile period, low planting density due to space needed for large free standing trees, the long generation cycles (from seed emergence to mature adult stage) and the need to evaluate fruiting characteristics over more than one season.

Certainly, the integration of quantitative genetics into kiwifruit plant breeding will enhance the possibilities of genetic advance and our ability to predict this advance. However, more genetical information needs to be accumulated before the benefits of quantitative genetics can be realised. More scientific studies, such as the current FMD study, must be initiated to increase the necessary body of scientific knowledge. The genetic information can be used to determine the best strategies to use for improving kiwifruit breeding and selection.

In a similar study, Burdon (1986) reviewed various aspects of the New Zealand Forest Breeding Programme and the relative importance of key research areas in comparison to other long-lived perennials (Table II-1). Burdon stressed the importance of developing efficient propagation methods, shortening generation times, and developing faster and more improved screening methods. These concerns are reiterated by Saure (1987) and by Ferguson *et al.*, (1996) for kiwifruit. Burdon (1986) proposed that such emphasis had allowed much progress in applying genetic theory and knowledge to enhance the efficiency and reduce the risks in New Zealand Forest Tree Breeding. Table II-1, illustrates the similarities and differences between the various breeding programmes.

Table II-1 : Relative merits to plant breeding of various features amongst long-lived perennials.

Problem / Feature	**Pinus Radiata**	**Apples**	**Kiwifruit**	**Rye[#] Grass**	**Lucerne**	**Wine grapes**
Generation interval	***	**	**		*	*
Evaluation time	**	***	***	*	*	***
Space requirement etc.	***	***	***	*	*	**
Crop replacement costs	***	**	**	*	**	***
Maturation (irreversibility)	***	**	***			
Virus infection	?	**	?	*?	*?	***

*** denotes extremely important * denotes minor importance.? denotes situation uncertain.
[#] = perennial ryegrass (Note: this is intended to illustrate the contrast among species rather then to attempt definitive statements for each case) from Burdon (1986).

Limitations to progress in kiwifruit breeding are similar to many other perennial species. The major constraints include the need for support structures, the inability to select immature plants (*i.e. during the juvenile phase*), polyploid variation and the lack of genetic information (Ferguson *et al.*, 1996). The polyploid variation in *Actinidia* restricts the chances of recombining different species (inter-specific hybrids) to produce new and novel arrangements of genes. Four ploidy levels (diploid, tetraploid, hexaploid, and octaploid) have been reported in *Actinidia*, including ploidy variation within taxa. Recent studies by Harvey *et al.,* (1991) investigated barriers to inter-specific hybrids.

Their results indicated incompatibility reactions were very important in determining the success of inter-specific crosses, with the major effects being genotype (of the egg bearing parent) and pollen quality.

The dioecious nature of *Actinidia* further complicates the kiwifruit breeding process. Staminate vines tend be more precocious (i.e. reach sexual maturity sooner) than pistillate vines, in the early part of the generation cycle at least, and the result is that some families tend to have 'male bias' in their sex ratio. However this male bias attenuates during the later stages of the generation cycle and in general once <u>all</u> vines reach full maturity, the pistillate and staminate vines tend to be present in almost equal number giving a sex ratio of 1:1 (Testolin *et al.,* 1995).

Kiwifruit seedlings used in this study are a result of controlled cross-pollination of female (pistillate) genotypes and male (staminate) genotypes. Because the genetic constitutions of all individual F_1 seedlings are equally dependent on both parental genotypes, it is reasonable to assume that the general performance of the full sib families for vegetative and fruiting characteristics represents the net effects of the gene recombination of their respective parental genotypes.

2. Juvenile period in perennial fruit crops

The lengthy generation cycle is the most serious problem facing many perennial fruit breeding programmes. All woody perennial fruit crops raised from seed require a certain period in years before the seedlings are able to flower; this is the *juvenile period* and can vary from 3 - 14 years depending on the plant species (Hansche, 1986; Alston and Spielgel-Roy, 1985; Hansche and Beres, 1980). Pears have a juvenile period of 7 - 14 years while apples typically have a juvenile period of 5 - 9 years. In contrast, kiwifruit are more precocious with a juvenile period of 3 - 7 years (Ferguson *et al.,* 1996; Hansche, 1986; Bringhurst, 1983; Visser, 1965; Saure, 1987). The NZKBP has been trying to reduce the generation cycle of *A. deliciosa* by extracting seeds from the fruit in early autumn and raising seedlings during the winter months, utilising glasshouse facilities with heating and artificial lighting.

This '*fast tracking*' method has been successful in reducing the *time to field planting* by one year. The '*conventional*' plant propagation method, in contrast to the '*fast track*' method, has a longer lead in period (pre-*field-planting*). Seed is extracted from the fruit in late autumn and sown in the following spring; these seedlings are grown during the summer months in a 'growing-on-line' nursery situation. The seedlings are then planted either in the following winter or spring, almost 12 months after germination. The Figure II-1, below, illustrates the contrast between these two propagation methods.

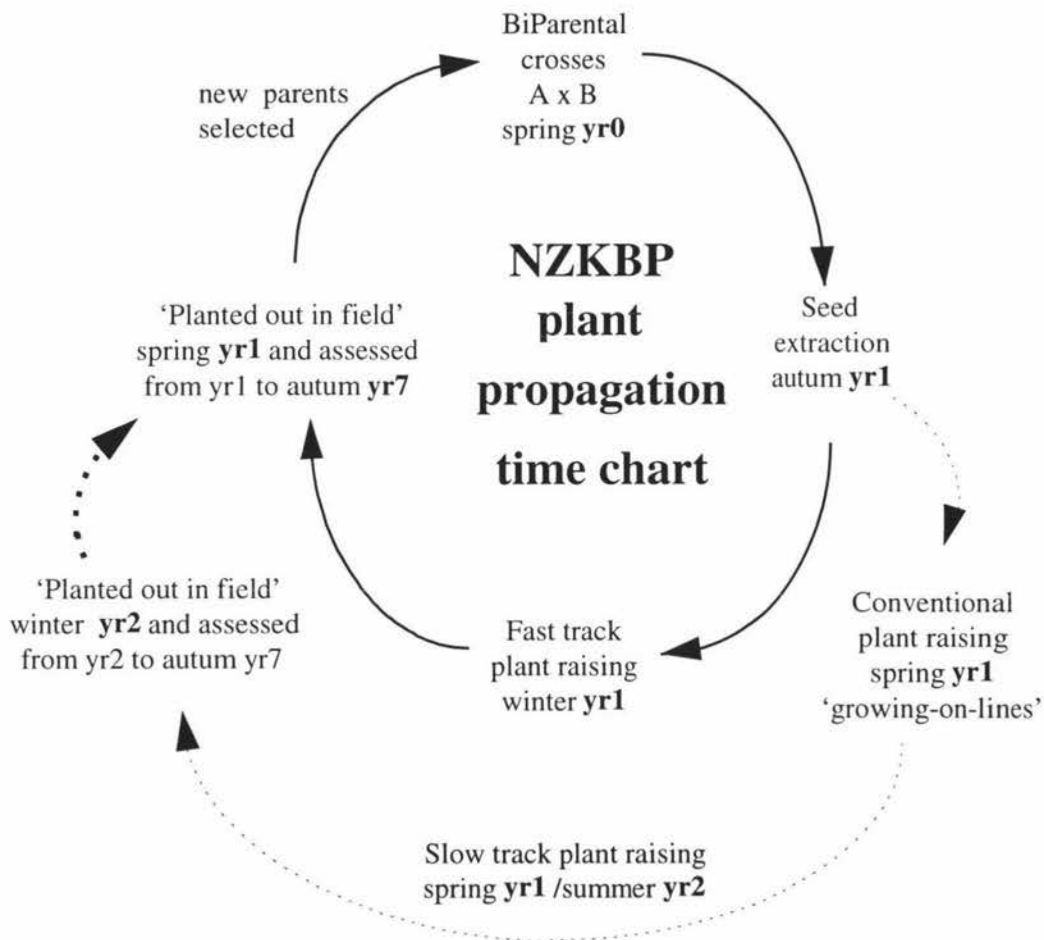


Figure II-1 *:* Flow chart of fast track and conventional plant propagation methods in the New Zealand Plant Breeding programme (NZKBP).

Although the *fast-tracking* method has an apparent advantage, the time from field planting to flowering may be little effected by the type of propagation method used. That is to say using either the fast track or conventional propagation methods may not reduce

the juvenile period itself. In contrast, shortening the seedlings' juvenile period by breeding for precocity has led to significant reductions in the generation cycle of other fruit tree crops. In order to utilise this approach in kiwifruit breeding, the amount of genetic variation involved in the juvenile period (or precocity) must be ascertained. Accordingly, some measurement must be made to quantify the character of precocity.

The perennial nature of *A. deliciosa* means sexually mature seedlings flower annually during spring of each year. Generally, most seedlings become sexually mature after 3-4 years from *field planting*. Therefore, it is logical to assume a datum (or starting point) as being that when the seedlings were planted out in the field i.e. spring 1992 in the FMD study. The time to first flowering would be in units of years from the datum point. This would allow a quantitative approach to analysing the inheritance of the juvenile period (Bell and Zimmerman, 1990).

Juvenility studies in other fruit tree crops have used various indirect measures of the juvenile period. These include flower and fruit numbers per plant, and morphological changes in leaf shape i.e. as plants progress from the "juvenile phase" to "adult" phase during ontogeny, (Visser 1965). In a study of the juvenile period of apples and pears a significant negative phenotypic correlation ($r = -0.52$) was reported between the vigour of seedlings (estimated by the trunk diameter in cm's) and their juvenile period (Visser, 1965). Visser (1965) concluded that increased vigour of seedlings had the correlated effect of reducing the juvenile period in apples and pears. In addition, if an "adult" selection was grafted or budded, then a certain amount of time would elapse (usually in years) before the clonally reproduced selection would flower and fruit. This was termed its' *vegetative period*. There was a strong phenotypic correlation ($r = 0.77$) between the *vegetative period* of the selections used as parents and the *juvenile period* of their progenies (Visser, 1965). As a result, Visser (1965) postulated that the selection of precocious parents could shorten the juvenile period of their progenies.

Precocity is axiomatic in many other plant species although there are no examples in the scientific literature, to the authors' knowledge, that illustrate the use of breeding for precocity (or juvenile period) as being applied to kiwifruit breeding. However, the ability to utilise precocity in this way will be dependent on how much variation exists for

precocity and the type of genetic control (either additive or non-additive) that there is in the inference base population of the *A. deliciosa* used in the FMD study.

Hansche and Beres (1980) reported two major barriers to genetic advance of fruit and nut tree crops, these are plant size and seedling juvenility. Their research suggested 'mass selection' was the most cost effective breeding method for these fruit tree crops. Hansche (1986), reported that the effect of the juvenile period was to limit the rate of genetic gain, suggesting an inverse relationship between the length of the generation cycle in years (T) and response (R) or genetic gain (Equation II-1)

$$\frac{R}{T} = h_n^2 \, i \, \frac{S}{T}$$

R = rate of response to selection, h^2 = narrow sense heritability estimate of a trait, ***i*** = selection intensity, ***S*** = estimated standard deviation (of phenotypic variation) and **T** = length of the generation cycle in years (Hansche, 1986).

Equation II-1 : Response (R) and generation time (T) in years.

In addition, almost 90% of the cost of maintaining and evaluating perennial breeding stock over several years occurred during this time (T). Therefore, longer generation cycles (T) incurred greater costs to the breeding programme which could significantly reduce genetic advance. Long juvenile periods would, therefore, carry a very high penalty (Hansche, 1986). The cost, to the NZKBP, of maintaining one hectare of kiwifruit seedlings (~1200 plants) in the field can vary from $13-17,000.[00] per year. This is the plant maintenance cost alone and does not include the cost of gathering information for plant genetics and selection work. Clearly, any opportunities to reduce the time of the generation cycle (and thus the cost incurred) have distinct and direct advantages to the kiwifruit breeding programme. However this is counter-balanced by the need to assess kiwifruit for more than one season, thus extending the generation cycle even further. In my experience the first and second years fruiting can be very different from the third (or later) years for several key traits such as fruit size, plant yield and fruit quality attributes.

Many fruit tree crops are known to have differences in fruit quality due to seasonal effects, fruit loading and carbohydrate partitioning during the plants growth and development (Tancred *et al.,* 1995; Hansche, 1986; Kester *et al.,* 1977; Hansche *et al.,*

1972; Hansche *et al.,* 1972a). As a result, the evaluation of kiwifruit pistillate progenies should be repeated for a minimum of at least two consecutive fruiting seasons (M. McNeilage, *pers. comm*), although, preferably, as many seasons data should be collected as possible.

Hansche (1986) also investigated the feasibility of reducing the juvenile period by selecting for more precocious parental genotypes in *Prunus persica.* The observed flower or fruit number per plant can be used as an indirect indicator for determining the effects of the juvenile period. Family means of fruit number per plant can be used to indicate relative differences in precocity. Those families with a mean fruit number of 2, for example, could be considered less precocious then those with a mean fruit number of 6. The narrow sense heritability for flower number per plant of $h^2_n = 0.16$, and fruit number per plant $h^2_n = 0.33$, were reported in *Prunus persica* breeding populations (Hansche, 1986). In this case, fruit number per plant is clearly influenced by both "environmental" and "additive genetical" components affecting the population. Consequently, both these factors must contribute to the length of the juvenile period. From these results, Hansche (1986) again suggested that the 'mass selection' procedure would be an effective breeding method for reducing the juvenile period from three to two years in the peach and nectarine breeding stocks at the University of California, Davis.

More recently, Bell and Zimmerman (1990) showed the juvenile period in several *Pyrus* species was inherited quantitatively, the parents differing in their ability to transmit shorter juvenile periods to their offspring. The general and specific combining abilities (GCA/SCA) for the juvenile period (expressed in years to first flowering), in these *Pyrus* species, were highly significant. The significance of the SCA component suggested that epistatic effects were also involved in determining the juvenile period of the various *Pyrus* species investigated. However, the GCA component was almost seven times greater than the SCA component. The magnitude of this difference suggested GCA had far more practicable importance indicating that it is also reasonable to assume that the juvenile period in *Pyrus* is predominantly controlled by additive gene action.

In juvenile studies of various *Citrus* species, Snowball *et al.*, (1994) reported that the main stem and seedling size, as opposed to the age of the plants, were significant in determining the juvenile period. This result was in agreement with Visser (1965) and

Hansche (1986) who indicated that seedling vigour and juvenile period were interrelated; in general those seedlings with more vigour had shorter juvenile periods. Juvenility studies in avocado (*Persea americana* Mill.), carried out by Lavi *et al*., (1992) indicated that although juvenility in avocado seedlings was influenced by environmental factors, there was still a significant contribution due to the genetic constitution of the seedlings. They concluded that the selection of precocious parents could significantly reduce the juvenile period. In addition, self-pollinated progenies of avocado were no different in their juvenile period behaviour, to those progenies that were cross pollinated, indicating no negative effect on precocity due to an increased inbreeding level in the self-pollinated avocado.

The results from these researchers confirmed earlier work by Visser (1976). The common finding amongst these studies was that the selection of parents with short juvenile periods, or with high positive GCA values (for an *indicative* trait used to estimate precocity), would be an efficient method in reducing the generation cycle in long lived perennial species i.e. *Pyrus* and *Malus*. In summary, there are many examples in the scientific literature of prolonged juvenility and in all of these cases two distinct disadvantages of increased juvenility are that it

- reduces the potential of crop improvement by increasing the generation time and therefore reducing genetic gain
- increases the cost of crop improvement, in almost direct proportion to the length of the juvenile period

Overcoming the juvenile period by selecting for early precocity could significantly increase the efficiency of the kiwifruit breeding programme, provided the juvenile period (or precocity) has an additive genetic basis i.e. it is heritable. Clearly, it is important to measure the juvenile period in the kiwifruit inference population in order to determine the nature of its inheritance.

B. Quantitative genetics in a factorial mating design

Generally quantitative genetic information in kiwifruit is scarce, with the most comprehensive publication by Zhu (1990) with other publications by Blanchet & Chartier (1991), Beatson (1991) and Testolin *et al.*, (1995). Quantitative genetic theory was first utilised by animal breeders, Lush, Dickerson and Hazel, during the 1930's. Plant breeders like Hull, Sprague, Comstock and Robinson began applying the new genetic theory to plants from the 1940's. Quantitative genetics deals with the inheritance of metric characters amongst related individuals. As a result, the metric characters are expressed in terms of *degrees of differences* as opposed to actual *qualitative* differences. Quantitative genetics allows plant breeders to determine the type of genetic variability present in a target population for a particular trait. Based on this genetic variation, the plant breeder can choose the most appropriate breeding method and selection strategy to achieve the plant breeding objectives (Cubero and Moreno-Gonzealez, 1993; Janick and Moore, 1983; Bringhurst, 1983; Moll and Struber, 1974).

1. Phenotypic variation of metric traits

Quantitative traits are assumed to be controlled by the same Mendelian segregation laws as those that affect qualitative traits. The critical difference is that *quantitative* traits are assumed to be determined by an unknown number of genes while *qualitative* traits are those where phenotypic differences can be explained by the action of one or two genes. Similarities have been shown to exist between the properties of polygenic traits and the classical Mendelian single gene traits, these include dominance, epistasis and linkage effects (Kearsey, 1993; Borojevic, 1990; Mayo, 1980).

Quantitative or metric traits are generally characterised by a continuous distribution. Phenotypic measurements from an individual plant or its fruit give an estimate (a statistic) of the phenotypic value (P) of the particular trait being measured. The phenotypic value of the trait is influenced by the individual's genotype (G) and its environment (E): the linear additive model is $P = G + E$ (Nyquist, 1991).

a) Phenotypic and environmental deviations

Falconer (1989), uses the terms genotypic value (G) and environmental deviation (E) for the two separate components that make up the phenotypic value (P). The genotypic component is determined by the genetic constitution of the F_1 seedlings, as a result of the random combination of gametes from both parents during the sexual process. The environmental component (E) includes all the non-genetic influences, which cause an individual F_1 seedling's phenotype to deviate from its genotypic value. Falconer (1989) terms this the 'environmental deviation' (E). Therefore, an individual F_1 seedlings' genotype confers a certain value (G) and the environment causes a deviation from this, in one direction or the other.

b) Population mean (M)

The phenotypic values of all the individual F_1 seedlings, in a breeding population, are used to estimate the population mean and the phenotypic variance (σ^2_p). The latter is derived from the mean sums of squares for each of the individuals phenotypic deviation from the overall population mean (M) (Falconer, 1989). Falconer (1989) begins his exposition of quantitative genetic theory with the single locus two-allele case, proposing that the population mean (M) can be determined by :

$$M = a(p - q) + 2pqd$$

The first term on the right-hand side, $a(p\text{-}q)$ is attributable to the homozygotes while $2pqd$ is attributable to the heterozygotes. The values a and d are derived from the gene model and represent the homozygote and heterozygote genotypic values. In addition the homozygote recessive is represented by $-a$ while the homozygote dominant is $+a$ in the gene model (see Falconer, 1989). The gene frequencies p and q (given $p = 1 - q$) in the population represent the proportion of the A_1 and A_2 alleles, where A_1 is dominant to A_2. The dominance value d can also influence the population mean dramatically; for example, where $d = 0$ (i.e. no dominance) the population mean M = $a(p\text{-}q)$; where $d = a$ (i.e. full dominance) M = $a(1\text{-}2q^2)$; where $d > a$ (i.e. over dominance) the population mean will fall outside of the range $\pm a$.

c) *Breeding value (A) and average allele concept*

The F_1 progeny derived from the genotypes of individuals used as parents, is considered to represent the assemblage of the parents genes. The genotypic performance of this progeny, when averaged for their phenotypic values across all possible environments, represents the *breeding value* (A) of the parents (Kearsey, 1993; Mayo, 1980; Falconer, 1989). This assumption requires that the environmental deviations must sum to zero, at which point the genotypic and phenotypic values are equal (Moll and Struber, 1974).

The *breeding value* of the parents will determine their genetic contribution to their offspring's genotypes (Kearsey, 1993). The parents pass on their genes not their genotypes to their offspring during the sexual process. An integral factor in the transmission of this genetic information, is the *average allele effect* (α), which is defined as the average effect of the parents' genes that determine the mean genotypic value of their progeny (Falconer, 1989).

Falconer (1989) describes the *breeding value* (A) as referring to an individual's genes, when used as a parent and not its genotype. The value associated with these genes, when transmitted to offspring, allows a *breeding value* (A) to be assigned to that individual when used as a parent. For a given character the average allele effect (α), involves the change in the population mean (M) that results from an allele substitution. In the single locus two allele case, with A_1 being the more allele and A_2 being the less allele, allele substitutions of A_1 for A_2 at random in the F_1 population produces the average allele effect. In addition, average allele effect can be defined as $\alpha = a + d(q-p)$, where a, p, q and d are defined as above. From the definition of α, it should be noted that its value is maximised when the frequency of A_2 alleles (q value) is at its highest, and conversely, when q is at its lowest then the average allele effect is diminished. Furthermore, A_1 allele substitutions can be described as $\alpha_{11} = q\alpha$, while A_2 allele substitutions can be equated to $\alpha_{22} = -p\alpha$, as defined by Falconer (1989). Clearly then, the average allele substitution for an A_1 allele is dependent on the A_2 allele frequency, and vice versa. The *breeding value* (A), in a single locus two allele case, can be estimated as the sum of twice the α_{11} or α_{22} for the homozygotes and $(q-p)\alpha$ for the heterozygotes.

The additive variance σ_a^2 of the *breeding values* can then be estimated, as a deviation from the population mean (M), by $(2p^2q\alpha + 2pq(q\text{-}p) - 2q^2p\alpha)$ i.e. multiplying each breeding value by their respective gene frequencies. The additive variance σ_a^2 is generated by each progeny's individual average allele effect (α). The additive variance is the chief cause of resemblance between relatives. The individual parent's mean value of its progeny, with respect to a particular trait in the population, determines the parent's breeding value.

Therefore the *breeding value* (A) is a property of the parent and the population from which its '*mates*' are drawn, while the average allele effect (α), is a property of the gene and the same population. Variation in the *breeding value* is sometimes described as the '*additive effects*' of the genes. However, this does not imply additive gene action in a strict incremental sense. In fact additive variance makes no assumptions with respect to gene action. In addition, the presence of dominance and/or epistasis does not necessarily preclude the possibility of additive gene action either (Falconer, 1989).

The genotypic value of an individual in a single locus two-allele case has two components; a proportion due to its *breeding value* (A) and a proportion due to the dominance deviation (D). Statistically the dominance deviation is an interaction term. The intra-locus interaction of the allelic pairs provides the dominance deviation (Falconer, 1989). The dominance deviation can be estimated from the difference between the genotypic value (G) and the *breeding value* (A). This model can also be applied to the digenic, trigenic or polygenic cases by the addition of a third term, the interaction or epistatic deviation (I).

$$G = A + D + I \qquad \textit{values} \qquad \sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_I^2 \qquad \textit{variances}$$

The epistatic or interaction effect is present when the inter-loci genes interact in combination with each other. The complex nature of these interactions is not as important as the overall effect when summed across many loci (Dudley and Moll, 1969). This latter point illustrates why the aggregate effect can be used in the genetical analysis of breeding populations.

Falconer (1989) showed the additive genetic variation could be described as

$$2pq[a + d(q - p)]^2$$

[*where p q a and d are defined above and the term in the square brackets is the average allele effect* (α)]

Similarly, the dominance genetic variance could also be described in terms of twice the allele frequencies of p and q multiplied by the heterozygote effect, all squared

$$[2pqd]^2$$

[*where p q and d are defined as above in the gene model*]

Therefore in a single locus two-allele case the additive, dominance and genotypic variances may be calculated on the basis of the gene model effects $\pm a$, d etc and their allele frequencies. It is evident therefore, that allele frequencies (p and q) are at the centre of the whole issue of genotypic variation in breeding populations; however, it is also important to note that these allelic frequencies must first be able to be measured. The types of quantitative traits measured in the FMD kiwifruit study have not allowed allelic frequencies to be estimated for the various characters. However, the concepts of additive and dominance genetic variation can equally be applied to the FMD study, from a variance component analysis of the factorial mating design populations.

2. Variance components and quantitative traits

There are many economically important traits of fruit tree crops i.e. yield, quality and maturity that are typical examples of quantitative traits (Bringhurst, 1983; Falconer, 1989; Mayo, 1980; Hansche and Beres, 1980). These quantitative traits have a complex nature particularly at the gene interaction level where many genes can have epistatic and/or dominance type interactions and are characterised by a continuous distribution of phenotypes. These traits are also assumed to be under the control of many genes (polygenic), as well as being influenced by the environment. (Kearsey, 1993; Falconer, 1989). In order to delineating these polygenic effects, Fisher developed a biometrical approach using *variance component analysis*, in 1918 (Hayward *et al.,* 1993).

Biometrical genetics developed from this, primarily concerned with the inheritance of quantitative traits. The basis of biometrical genetics is the relatives' variance and covariance analyses, used to determine the genetic properties of a breeding population.

Mather (1941) described the continuous variation of quantitative traits as "the result of the joint action of a number of supplementary genes each contributing a small effect, in relation to the total variation observed", this was later termed 'polygenic variation' by Mather (Hayward and Breese, 1993).

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2$$

where,

$$\sigma_G^2 = \sigma_{Ga}^2 + \sigma_{Gna}^2$$

Equation II-2 : Phenotypic, genetic (additive & non-additive) and environmental variation

Phenotypic variation (σ_p^2) in a plant population is, therefore, the sum of the squared deviations of <u>all individuals'</u> genotypic (G) and environmental (E) contributions, towards the total variance (Falconer, 1989; Mayo, 1980). In addition, the genetic component (σ_G^2) can be further partitioned into additive and non-additive genetic contributions as in where σ_p^2 = phenotypic variation, σ_G^2 = total genotypic variation, σ_E^2= environmental variation and (σ_{Ga}^2) & (σ_{Gna}^2) = additive & non-additive genetic variation. The latter two components form the basis of the genetic variation in the population, which is of prime importance to the plant breeder. The breeding population must have a reasonable amount of σ_G^2 in order for genetic advance to continue and a significant proportion of the total genetic variation should be of an additive nature (Kearsey, 1993; Borojevic, 1990; Falconer, 1989). In the case of a trait controlled by one locus and two alleles, the additive variance component is made up of the intra-locus additive effects $\sigma_G^2 = \sigma_a^2$ while the non-additive portion, only represents the intra-locus dominance effects σ_D^2 (Falconer, 1989).

Alternatively, if one assumes that several loci (with two alleles each) are acting on a trait, then the genetic components also include epistatic or interaction effects (inter-loci) $\sigma_{Gna}^2 = \sigma_D^2 + \sigma_{AA}^2 + \sigma_{DD}^2 + \sigma_{AD}^2$. Quantitative plant breeding utilises various 'mating designs' in order to partition the total phenotypic variation into these two major

components, σ_G^2& σ_E^2. Some experimental 'mating designs' available include the bi-parental, diallel (four types) and factorial mating designs (Kearsey, 1993; Hayward *et al.*, 1993). The simple linear model described above, in Equation II-2, does not consider the problem of genotype by environment (*GxE*) interaction. Falconer (1989) reported that the correlation between genotype and environment is of little significance in an experiment that has a randomised complete block design. The author suggesting that the *GxE* correlation component could be neglected, although still unavoidably present in the estimation of the σ_G^2 (Kearsey, 1993; Hayward *et al.*, 1993; Nyquist, 1991). Falconer (1989) showed that is possible to partition out the *GxE* interaction component by the use of a two-way (genotype and environment) crossed classification experiment.

A series of papers by Hansche *et al.*, from 1965 to 1975, investigated various aspects of temporal and spatial replication in experimental design in an attempt to reduce the effects of yearly climatic variation on various traits in sweet cherry (*Prunus avium* L). A least squares method was used to adjust the data for yearly climatic differences; Searle and Henderson described this method in 1961. Random fluctuations in yearly climatic conditions are well known to affect the performance of the progeny. This also hinders the plant breeders' efforts in discriminating the best genotypes to select. Hansche *et al.*, from 1965 to 1975 suggested that the use of crude subjective measurements with high variability was associated with, and led to lower heritability estimates (Hansche *et al.*, 1975; Hansche *et al.*, 1972; Hansche and Brooks, 1965; Hansche and Beres, 1965; Hansche *et al.*, 1965).

3. Factorial mating design

Various mating designs are used to create a family structure (of relatives) for genetic studies in plant populations. These familial relationships allow the plant breeder to estimate various genetical components from the overall phenotypic or observed variance. These estimates indicate the presence of genetic variation in the breeding population. The term, mating design, refers to the system of mating used to develop progenies. Cockerham (1963) clarifies mating designs as one, two, three or four factor designs dependent on the number of ancestors per progeny over which control is exercised. The use of a simple half sib set of families or polycross progenies in an single-factor design would be sufficient to detect the presence of genetic variability.

Estimation of additive and dominance variation (assuming no epistasis present) must utilise a two-factor mating design. In addition, the estimation of epistatic variance requires a more complex design or combination of designs to be employed. The genetic components of variance, estimated from these mating designs, can be equated to covariances of relatives (see Chapter 3 - Materials and Methods). This can be achieved by translating the ANOVA of readily analysed data into covariances of relatives; these covariances are then equated to particular genetical components. In addition, statistics such as the additive and non-additive genetical variance components and their standard errors can then be estimated (Kearsey, 1993; Hayward *et al.,* 1993; Nyquist, 1991).

The dioecious nature of the *Actinidia deliciosa* species restricts the use of full, half or partial diallel designs for genetic studies. The factorial mating design (FMD) was considered the most appropriate experimental design given this biological constraint of the *A. deliciosa* species and the type of genetical information required. The FMD design is based on the North Carolina Model II (NCMII) design, described by Comstock and Robinson (1948). The FMD has the advantage of increased number of parents being sampled from the base germplasm pool, without increasing the experimental size, especially when compared to the full diallel case (Hallauer & Miranda, 1981).

Other advantages considered important in choosing the FMD for *A. deliciosa* include:

- two independent covariance estimates for calculating the additive genetic variance component
- two estimates of GCA for female and male effects and a test for SCA, female x male, interaction effects
- independent covariance estimate of the degree of dominance of a trait (assuming no epistasis present)
- a test for the presence of maternal and paternal effects can be estimated.

Kearsey (1965) presented a comprehensive review on the efficiencies of five biometrical mating designs and the types of genetic information they provided, using random mating populations of *Papaver dubium*, long head poppy. The summary of Kearseys' (1965) results listed the advantages and disadvantages of each system. It was clear from these results that specific designs should be chosen in order to estimate predetermined genetic information, also the simplest design that supplies the required information is the best option.

Accordingly, Kearsey (1965) suggested in selecting an appropriate mating design the plant breeder must consider both the reproductive mode of the crop species and the resources available to the plant breeding programme. A more recent review by Christie and Shuttack (1995) on various diallel designs and their use in plant breeding, also confirmed Kearseys' findings.

In contrast, Kearsey (1965) reported the NCMII was adequate in discerning the additive genetic variance but was seriously affected in its estimation of the epistatic effects (non-additive variance). Kearsey (1965) was able to determine significant non-additive interaction by the use of the Hayman's modified half diallel (Jinks and Hayman, 1953). Clearly, the interpretation of the dominance variance in the FMD of this study should be treated with caution, although, Kearsey's (1965) results did illustrate that the North Carolina models were the most effective in separating the total genetic variation from the residual error.

4. Covariance of relatives

Fisher (1918) was the first to report the partitioning of the total phenotypic variation into additive, dominance and epistatic variance components. Since then several refinements have been added to, clarified and extended by many biometricians such as Crump, Eiesenhart, Gallias, Kempthorne and Cockerham as examples (Nyquist, 1991; Hallauer and Miranda, 1981; Moll and Struber, 1974; Kearsey, 1965; Henderson, 1953).

The theoretical basis for the covariance of relatives depends on the genetic resemblance between relatives. The covariance of relatives, indicates how relatives vary together, and is calculated by using the statistical method of covariance analyses. The genetic basis for the likeness between two phenotypes in a population is dependent on the similarities in their individual genotypic values (Hallauer and Miranda, 1981). The resemblance between relatives is a basic genetic phenomenon of metric traits and is therefore a property of the character being measured. The additive genetic variance determines the degree of resemblance between relatives (Hayward *et al.,* 1993). Clearly, selection for a character with a high component of additive genetic variation (high heritability) would be expected to perpetuate through its filial generations (Wricke and Weber, 1986).

Simple quantitative measurements of metric characters, in a breeding population with a known family structure (relatives) allow sources of variation (SOV) to be classified based on these types of relatives. These familial classifiers and their associated variance components can be equated to their respective covariance of relatives, as in Table II-2. Accordingly, the covariance and its associated genetical interpretation can take on various meanings dependent on the type of relationship being described. The FMD study has a two way classification of progenies. The first main effect (A) is the female parental array, which estimates the covariance of half sibs based on the female parent. The second main effect (B) is the male parental array which estimates the covariance of half sibs based on the male parent. These variance components also enable a test for GCA and its significance, based on either factor A or B (female or male). The advantage of the two-way classification is an estimate of either maternal or paternal GCA effects on various characters (Becker, 1992). This is especially useful in the genetic studies of kiwifruit, as the influence of male parents genes on the fruiting characteristics of its female progeny

needs to be determined (Testolin *et al.,* 1995). The contribution of the male parent vines to the fruiting characters of its female progeny has yet to be determined. This currently means only half the genetic variance can be utilised (Ferguson *et al.,* 1996; Testolin *et al.,* 1995; Beatson, 1991). Testolin *et al.,* (1995) strongly recommended the need to determine the effects of the staminate parent on the fruiting characters of its female progenies, by indirect selection indices. This would allow the full utilisation of both the pistillate and staminate parents' contribution to the genetic variance of their offspring.

The genotypic value of an individual cannot be measured directly. However, its phenotype can be measured and the phenotypic covariance between two relatives estimated. The use of appropriate experimental design (and randomisation) to partition out the environmental variances (*GxE* and *E*), then allows the Cov(Px, Py) to be estimated (Nyquist, 1991).

$$\underset{\text{(phenotypic covariance)}}{\mathrm{Cov(Px,\ Py)}} = \underline{\mathrm{Cov(Gx,\ Gy\ )}} + \mathrm{Cov(GEx,\ GEy\ )} + \mathrm{Cov(Ex,\ Ey\ )}$$

and

$$\underset{\text{(genetic covariance)}}{\mathrm{Cov(Gx,\ Gy)}} = r\,\sigma^2_{A} + u\,\sigma^2_{D} + r^2\,\sigma^2_{AA} + ru\,\sigma^2_{AD} + u^2\,\sigma^2_{DD} + r^3\,\sigma^2_{AAA}.$$

Equation II-3 : Estimates of phenotypic covariance of relatives and genetic covariance of relatives as a linear function of their genetic variance components (from Nyquist, 1991).

The values of r and u for half sib relatives is ¼ and 0 respectively, while for full sib relatives, the values are ½ and ¼ respectively. Substituting these values into Equation II-3, derives the various coefficients of which the covariance of relatives are equated to for a large random mating population. Note the epistatic variance components from term 3 on the right hand side of the equation.

The following Table II-2, lists the covariance of half sib values (for female and male arrays) and their expected coefficients for genetical variance components; for specific use in a FMD experiment (modified from Becker, 1992).

Table II-2 : Covariances and genetical variances of relatives (from Becker 1992).

Covariance	**Source of variation**	σ^2_A	σ^2_D	σ^2_{AA}
Cov $(HS)_{fem.}$	Female	$^1/_4$	-	$^1/_{16}$
Cov $(HS)_{male}$	Male	$^1/_4$	-	$^1/_{16}$
Cov $(HS)_{fem.\ x\ male}$ = [Cov(FS) – Cov(HS)fem - Cov(HS)male]	Fem. x Male	-	$^1/_4$	$^1/_8$
Total –Cov$(FS)_{fam.}$	Error (a)	$^1/_2$	$^3/_4$	$^3/_4$

The degree of resemblance between relatives is the 'between group' component of variance as a proportion of the total variance. This is also known as the intra-class correlation *t* (Falconer, 1989). The intra-class correlation *t* estimates ½ the additive genetic variance for full sibs (plus the non-additive portions) and estimates ¼ the additive genetic variance for half sib relatives. Accordingly, each method provides an estimate of the narrow sense heritability; with full sibs $\geq$ ½ h^2_n and half sibs = ¼ h^2_n.

Another method of estimating resemblance of parents and their offspring is known as parent-offspring' regression (POR). This method uses the mean trait of the parent, paired to the mean of its' offspring; alternatively the mean of the two parents b_{OP}, is paired to the mean of its' offspring. The former being *parent-offspring* (estimates ½ h^2_n) and the latter being *mid-parent-offspring* regression (estimates h^2_n).

The precision of these estimates from the correlation and regression methods can vary depending on several factors; certainly the failure of one or more of the above mentioned genetical assumptions (page 27) can have serious implications. As an example, failure of the assumption of no epistasis will in fact lead to an over estimate in the dominance variance component σ^2_D. These and several other considerations have been discussed by Kearsey, (1965); Jinks, (1981) and also Hayward *et al*., (1993).

C. *Heritability estimates and their precision*

Selection for pistillate vines is the main aim of any kiwifruit breeding programme. The contribution of the staminate (female) parent to the fruiting characters of its female progeny, can be found directly from the parent offspring regression method (POR) (Falconer, 1989). However, the POR method requires a replicated experimental design involving both the pistillate parental vines, as well as their progeny families. The advantage of the parent offspring method is its confirmation of the validity of the genetic results derived from the covariance of relative's method. The POR method of heritability estimation was not used in the current FMD study.

Falconer (1989) defines 'heritability' as the ratio of additive genetic variance to the total phenotypic variance ('narrow sense'), and any reference to heritability in the FMD study will be assumed to mean this unless otherwise stated. It is the underlying 'additive variation' that the plant breeder seeks to exploit in an attempt to maximise genetic gain.

Hanson (1963) considered various forms of heritability in plant selection work. These included narrow and broad sense heritabilities based on single plants, single plots or reference (sample) plots. Hanson (1963) suggested standardisation of the concept of heritability was necessary. However, Hanson (1963) realised the importance of a flexible definition in plant selection work and he illustrated two clear directives with respect to heritability and plant selection

- that heritability should be based on selection concepts
- reference material, selection unit (to which it pertains) and an obligation to present the estimated variance components, must preface heritability. Narrow sense heritability has the primary value of quantifying the expected progress from selection of a certain trait

If data is collected on an individual plant basis (as it is in the FMD study), then these plants form the basic "selection unit" from which the heritability is estimated. Hallauer and Miranda (1981) describe this as the individual plant heritability estimate.

The formula for estimating the heritability on an individual plant basis in a factorial mating design (i.e. NCMII) is given by

$$h^2_{ind.f(m)} = \frac{4\sigma^2_{f(m)}}{\sigma^2_w + \sigma^2 + \sigma^2_{fm} + \sigma^2_f + \sigma^2_m}$$

Equation II-4 : Heritability based on an individual plant basis (Hallauer & Miranda, 1981)

The variance components in equation II-5 (below), from Hallauer and Miranda (1981), also estimate the heritability on a mean entry basis, which in effect is the mean parental array heritability of the female (factor A). In a similar manner, the entry-mean basis for the male (factor B) parental array can also be estimated. The calculation of the mean entry by female (or male) parental arrays is given by Hallauer and Miranda (1981) :

$$h^2_{f(m)} = \frac{4\sigma^2_{f(m)}}{\frac{\sigma^2}{r\,m} + \frac{4\sigma^2_{fm}}{m} + 4\sigma^2_{f(m)}}$$

Equation II-5: Heritability based on entry-mean basis for female (or male) parental array (Hallauer & Miranda, 1981).

Therefore, the two-way classification (FMD) allows two independent estimates of the additive genetic variance to be derived by using either the female or male variance estimate. Alternatively, if the number of female (factor A) and male (factor B) parents are equal, the pooling of their respective sum of squares and degrees of freedom can be used to estimate a combined effect. However, the standard error for this pooled heritability estimate must have the numerator pre-multiplied by 2 instead of 4, due to the increased degrees of freedom in the denominator estimate.

1. Genetic variation and predicted response

Ascertaining the relative contributions of the total genetic variance, into additive and non-additive components, determines both the *descriptive* or broad sense heritability, $h_b^2 = \sigma_G^2 / \sigma_p^2$ and the *predictive* or narrow sense heritability $h_n^2 = \sigma_A^2 / \sigma_p^2$ (Kearsey, 1993; Falconer, 1989; Mayo, 1980). Generally, the *predictive* or narrow sense h^2_n is more useful in calculating the genetic gain (R). Estimating the genetic gain (or response), by Equation II-6, can be done as follows, where i = selection intensity, h^2_n = narrow sense heritability and σ_p = std. deviate of the population. This is also known as the predicted response (R) to selection. Plant breeding is primarily concerned with producing and selecting superior genotypes. The plant breeder must first define target traits for improvement and determine how these target traits can be improved and modified in subsequent generations.

$$R = i \ h_n^2 \ \sigma_{\mathrm{p}}$$

Equation II-6 : Response (R) or genetic gain.

The phenotypic expression of the progenies can be directed, with appropriate breeding methods and selection strategies, toward the plant breeders' goals by genetic manipulation *viz.* genetic gain. Heritability is a property of the phenotypic performances of relatives in a particular environment(s), for any measured character. From this definition, heritability is also a property of the population *per se* being studied (Falconer, 1989). Consequently, changes in any one particular variance component, can affect the final value of the heritability (Hayward *et al.,* 1993; Mayo, 1980; Hanson, 1963). Heritability, therefore, should not be considered a fixed parameter, but instead, should be considered as dynamic and variable as the components that define it. Very few authors have reported heritability for traits in kiwifruit (Testolin *et al.,* 1995; Beatson, 1991; Zhu, 1990). Heritability estimates from the 1996 FMD study, *may* or *may not* be in agreement with those previously reported. These discrepancies will be due, in part, to the violation of any of the basic assumptions used to estimate the genetic components and the precision of these estimates. In addition, the reference population (inference base) is based on a much broader germplasm then those previously reported in the literature.

2. Precision of heritability estimates

Heritability in both the broad and narrow sense has been used to describe the genetic variability in quantitative plant genetics. These heritability estimates are based either on single plants, plot averages or as samples (reference) of plots (Hanson, 1963). Plant breeders are interested in heritability in terms of selection. Allard (1960) described the practical use of quantitative genetic theory, to plant breeding, in its prediction of genetic advance or response (R). The effectiveness of the narrow sense heritability (h^2_n), used in prediction of response, depends on how reliable the h^2_n estimate is. If the additive genetic variance has been over estimated, the expected response will also be overestimated and can, therefore, mislead the plant breeder. It is crucial that the additive genetic variance is estimated with as much precision as possible. The parent offspring regression method (POR) when carried out concurrently with the population/covariance of relative's approach (FMD), augments the precision of these heritability estimates. Generally, the covariance of relatives estimate sets an upper limit to the heritability, especially if linkage and/or epistasis are present (Falconer, 1989). However during the planning of the FMD study there was no consideration given to a concurrent trial involving the parents for the POR method.

Furthermore, if these replicated parental clones had been established; then a better estimate of the genetic and environmental variances for the measured traits would have been available. This would also have allowed a more reliable estimate of the genetic fraction (*gkg*). Hanson (1963) noted the POR method, while being a straightforward technique, could not alleviate the bias due to genotype by environment interaction. In addition, the heritability could exceed 1.0 in cases where the genotype by environment was significantly large. Estimates of genetic variances based on individual plant variability could also be seriously affected in the case where interplant competition was a factor. As previously discussed, violations of the genetical assumptions in the estimation of the variance components can bias these observed estimates (statistics). Potentially, however, the greatest source of variation in the bias of heritability estimates, comes from the interaction of the genotype and environment main effects i.e. *GxE* (Kearsey and Pooni, 1996; Borojevic, 1990).

However it is possible, in carefully planned plant breeding programmes, to utilise certain designs to remove this source of variation. Clearly, any source of variation that leads to an imprecise measurement of the true additive genetic component will compromise the predictive nature of these estimates. Therefore, it's imperative that a well designed and appropriate experimental model is used in order to improve the estimate of the additive genetic component.

a) Estimation of a variance component

Variance components are estimated from the mean squares relevant to a particular experimental design. These expected mean squares (EMS) are independent linear combinations of variance components. The univariate analysis of variance is based on the linear additive model, whereby, the total sums of squares is partitioned by the principle of least squares (Steel and Torrie, 1980). In quantitative genetics the sources of variation are from random effects. There are two types of variance components: *statistical*, i.e. between clones, lines, half sibs or within plots, and the *genetic* and/or *non-genetic* (environmental) variances σ^2_a, σ^2_d , σ^2_{aa}, ... σ^2_e. (Wricke and Weber 1986). The additive genetic variance (for the FMD study) has two independent estimators based on either the female or male classifiers i.e. half-sib families. Wricke and Weber (1986) reported differences in inbreeding levels between these two main sources of variation could lead to difference variance components i.e. $Cov(HS_f) \neq Cov(HS_m)$. This is also evident from the fact that the additive variance has a coefficient based on the inbreeding level as a premultiplier (see Wricke and Weber, 1986). The FMD study has a reference population with varied levels of inbreeding (data not shown). In many instances, the exact pedigree and relationships between most parents is unclear. However, a few parental genotypes have a known relationship amongst each other, although, in general the inbreeding coefficients have been ignored. It is important to note, that differences between $Cov(HS_f)$ and $Cov(HS_m)$ may not only indicate maternal or paternal effects. Alternatively, these differences may be due to the differences in the level of inbreeding amongst these parents.

b) Standard error of the variance

The distribution of variance components is *not normally distributed* and cannot be fully described by the mean and variance. The variance of a variance component can be estimated from the mean squares that define the component itself. However, it is assumed that the mean square MS_j (or that mean squares of a linear combination) are independently distributed and follow a chi squared distribution that is twice its degrees of freedom i.e. $2f_1$. Therefore the well known variance component estimator is derived as follows -

$$\frac{SS_j}{E(MS_j)} = V(MS_j) = 2f_j \frac{[E(MS_j)]^2}{f_j^2} = \frac{2[E(MS_j)]^2}{f_j}$$

Equation II-7 : Estimate of the standard deviation (or variance) of a variance

Evidently, the unbiased estimator of the variance of a variance component $V(\sigma_t^2)$ can also be derived by -

$$V(\sigma_t^2) = \frac{1}{n^2} \sum_j 2 \frac{[E(MS_j)]^2}{f_j + 2}$$

MS_j = j^{th} mean square in the linear mean squares function
σ_t^2 = the tth variance component (having its variance) being estimated
n = the divisor appropriate to the estimator of σ_t^2
f_j = degrees of freedom of the jth mean square
+2 = an unbiased estimator of the variance of a variance (Searle, 1971)

Equation II-8 : Estimate of the standard error of a variance

Gordon *et al.*, (1972) reports some debate exists in the literature with regards to the +2 (correction for bias) factor, although, Searle (1971) offers an derivation. However, all variance estimators in the FMD study will use this unbiased correction factor in their calculations. The standard error is, therefore, the square root of the variance of the variance component. In the event of a constant been pre-multiplied to either MS_j (in the linear independent mean square function) then this constant is taken in the numerator of the first term (on right hand side of Equation II-8) and is also squared (see Wricke and Weber, 1986).

c) *Variance of a heritability (ratio of mean squares)*

Statistics involving ratios of variance components, i.e. heritabilities, generally have a large but unknown standard error. Certainly, to determine their standard errors with any precision is very difficult. Jensen and Barr (1971) reported several approximation formulae are available i.e. Graybill *et al.*, (1956), Henderson (1969), Osborne and Paterson (1952). These approximation formulae all require equal subclasses, but in most cases of biological data there is a failure in meeting this requirement.

Searle (1958) derived expressions that could be applied to determining standard errors of heritabilities. However, Searle's method assumes mean squares are independent and that the variance - covariance matrix of mean squares is a diagonal matrix. In addition, the off diagonal elements are zero when there are equal subclass numbers, although this is not the case for unequal subclasses. Searle (1958) appears to be the first to derive exact equations for the unequal subclass case. However, the procedure uses sums of squares and has a large number of calculations in order to arrive at a solution for the approximation. Osborne and Paterson (1952) suggested an approximate estimation of the variance of heritability, $V=y/z$ for continuous variables to be given by -

$$\sigma_v^2 \cong \left[\bar{z}^2\sigma_y^2+\bar{y}^2\sigma_z^2-2\,\bar{y}\,\bar{z}\,\mathrm{cov}(y,z)\right]/\bar{z}^4$$

where

$\bar{y}$ & $\bar{z}$ = expected values of genetic and phenotypic linear functions of mean squares (& are dependent on type of heritability defined)

$\sigma_y^{\ 2}$ & $\sigma_z^{\ 2}$ = variances of the linear functions of mean squares for y and z

Cov(y,z) = is the covariance of the respective mean squares in numerator and denominator of heritability statement

Equation II-9 : Variance estimate for heritability ratio from Osborne and Paterson (1952)

Osborne and Paterson (1952) indicated the approximation formula was only appropriate if the ratio of coefficient of variation (*c.v*) of the phenotypic variance σ_z divided by the mean phenotypic variance $\bar{z}$; was sufficiently small that powers greater than the first could be neglected. Where the value of $(\sigma_z/\bar{z})$ to the powers greater than 1 are not negligible this can lead to rather large estimates of standard errors.

The distribution of the estimates of heritability variance ratios was considered non-normal. However, Osborne and Paterson (1952) suggested construction of confidence intervals was still suitable. Jensen and Barr (1971) reported that the standard errors as estimated by Searles' method and Osborne and Patersons' approximation method, were in agreement with empirical results, but the differences between the two former approximation formulae was dependent on the number of observations per subclass. Hallauer and Miranda (1981), use a simple but conservative estimate approach to the standard error of a variance ratio h^2, by using Dickerson's method (1969). This approximation method was presented as a simplified formula based on Graybill *et al.,* (1956) and in Graybill and Robertson (1957). The formula ignores the terms involving the variance in the denominator as well as ignoring the covariance of the two terms.

$$V(\sigma^2_c) = \sigma^2_c / (2*\sigma^2_c + k\,\sigma^2_e)$$

σ_c^2 = expected values of genetic and/or phenotypic linear functions of mean squares (dependent on type of heritability defined)
σ_e^2 = variances of the linear functions of mean squares in total including the error
k = is the coefficient of the respective mean squares in numerator and denominator of heritability statement

Equation II-10 : Variance estimate for heritability ratio from Dickerson In: Hallauer and Miranda, (1981).

However, the standard error estimates from this method (above) are easier and quicker to calculate in comparison to the covariance approach (Equation II-9) and are somewhat more conservative (empirical data not shown). Therefore the Dickerson's (1969) method is used for the FMD study.

D. General and specific combining abilities

General combining ability (GCA_{mean}) is a measure of the '*general worth*' of the parents' gamete contribution across their respective progenies (Simmonds 1979). The mean performance of a particular series of crosses (half or full sib) represents its GCA_{mean} value for the parental array, when expressed as a deviation from the overall population mean (Falconer, 1989). In the FMD study the GCA mean performance of either parent (male or female) can be calculated from the parental arrays. Specific combining ability (SCA_{mean}) is an extra deviation from the expected mean value (GCA_{mean}) for a particular cross i.e. hybrid performance. Therefore the measure of '*general worth*' can be statistically based as deviations from the population mean (as stated above). Alternatively, the '*general worth*' can also be measured by the 'analysis of variance' procedure, which can then be interpreted by the covariance of relatives on a genetical basis. The two methods each have their application in an applied breeding programme but for different reasons. It is important to distinguish the difference between these two measures of '*general worth*' as explained by the mean performance (statistically based as deviations from the mean) versus the analysis of variance (GCA_{var}).

1. Combining ability and mean performance

The combining abilities for the FMD study provide an empirical summary of complex observations. These summaries are based on first degree statistics (marginal totals and means). Generally, these statistics are more robust than those of the previous sections involving variance components i.e. second degree statistics (Hayward *et al.,* 1993; Nyquist, 1991). Combining abilities are not based on any genetical assumptions and should not, strictly, be equated to the additive genetic variances or the GCA main effects, such as those in the ANOVA tables of Chapter 3. In an analogous fashion to heritabilities, the GCA means information should only be used when considering the specific inference base population and the particular experimental design used to arrive at these estimates. Combining abilities, therefore, can be used to predict the best performance of hybrid populations amongst the individual (BiP) biparental combinations in the FMD study.

a) GCA estimation from family means

Simmonds (1979) described the essential elements of a series of biparental crosses (BiP's) in very simple terms as

- how much variation amongst BiP's could be attributable to statistically additive features (*similar to the GCA main effects*) of parents
- how much variation amongst BiP's could be attributable to the residual interactions (*similar to SCA of main effects interaction*) of specific BiP combinations

These GCA/SCA mean values are very useful in an applied plant breeding programme such as the NZKBP. The difficulties involved in deciding which are the best individual parents to select (i.e. best breeding value) for a given character, is partially overcome by using GCA means based summary information. Certainly, predicting the best parental combinations (full sib families) from the FMD study can be facilitated by the use of these GCA means tables. The statistical expressions for these two estimates of mean effects are based on their GCA_{mean} and SCA_{mean} performance. These involve the following model and are estimated as deviations from the mean

$$X_{AB} = \overline{X} + G_A + G_B + S_{AB}$$

where

X_{AB}	=	BiP mean of A x B parent
$\overline{X}$	=	Grand mean (average of means)
G_A	=	GCA_{mean} of parent A (statistically the additive part)
G_B	=	GCA_{mean} of parent B (statistically the interaction)
S_{AB}	=	SCA_{mean} of BiP combination of parent A x B (statistically the residual interaction)

Equation II-11 : GCA/SCA means approximation formulae (from Simmonds, 1979).

The family (BiP's) means are estimated using the unweighted Least Squares Means (LSM's) in the GLM procedure of SAS®. These LSM's are estimates of the marginal means from unbalanced data, that might be expected had the data been balanced (Littell *et al.,* 1991). The internal imbalance is negligible for the vegetative characters; in contrast however, it is far more serious in the data analyses of fruiting characters (see Chapter 3).

2. Combining ability and variance analysis

The familial structure of a factorial design (e.g. FMD in this study) allows a two-way classification of these GCA main effects by either female or male parental arrays. The GLM analysis of variance procedure in SAS® is used to partition these GCA main effects for the respective parents in a factorial mating design and provides a significance test for these sources of variation. These will be referred to as '*variance based* GCA effects' or GCA_{var} in the FMD study. The GCA_{var} effects represent the variance due to the additive genetic variance (including, if present, a proportion of all 'additive by additive interactions' between other loci). The GCA_{var} effects source of variation is determined for both the male and female arrays and is expected to increase linearly as inbreeding levels (*F*) increase (Falconer, 1989). In the case of no maternal effects (or sex-linked characters), then male GCA_{var} effects = female GCA_{var} effects. Additionally, the factorial mating design also has a test for specific combining ability (SCA). The '*variance based* SCA effect' or SCA_{var} effects (as it will be referred to) represents the variance amongst parental arrays due to the non-additive genetic variance (dominance and/or epistatic effects) from particular combinations of BiP's (biparentals). Falconer (1989) indicates that it is in fact the SCA_{var} effect that is expected to increase variation as the inbreeding level (*F*) increases.

Therefore it is possible to assess the staminate (male) parental effects as well as the pistillate parental effects. The sub-group of half sib families based on either maternal (female) or paternal (male) lineage provides the classification of progenies into their respective parental arrays. Testolin *et al.*, (1995), used a factorial design in kiwifruit and concluded that further investigation was needed into the staminate (male) parental genotypes effects on their female (pistillate) progeny in particular. As indicated above, the staminate parent is equally important in determining the genetic constitution of the seedling. Therefore, in the instances where there are no sex-linked fruiting characters, the staminate parents could be tested for their GCA_{var} effects on fruiting characters. This would allow sib selection of male parents based on their effects on fruiting characters.

E. Phenotypic and genetic correlations

1. Phenotypic (simple) correlations

Correlation is the measure of the degree to which two variables vary together. The correlation is known as the product moment correlation or the simple correlation. The simple correlation can be used for descriptive purposes and is given by

$$r = \frac{COV_{xy}}{\sqrt{\sigma_x^2 \sigma_y^2}}$$

$COVxy$ = covariance of x and y

$\sigma^2_{x/y}$ = variance of attributes x and y

Equation II-12 : Correlation (simple or product moment) coefficient formulae from Steel and Torrie, 1980.

The simple correlation coefficient, *r*, is independent of any unit of measure i.e. dimensionless (Steel and Torrie, 1980). Searle and Henderson (1961) described the phenotypic correlation as the product moment correlation of two characters measured on the same individual plant. Many quantitative characters are correlated to other characters (Hayward *et al.,* 1993). Falconer (1989) defines phenotypic correlation, r_p, between two characters as having two major causes:

- genetic correlation r_a - the correlation of breeding values due to pleiotrophy (i.e. metabolic interdependence) or sometimes linkage (in divergent line crosses)

- environmental correlation r_e - the degree to which two characters are influenced by changes in their shared environment.

The phenotypic correlations (r_p) of relatives for a single character correlated with another (second character) can therefore be partitioned in various sources of variation. Consequently, Falconer (1989) defined the phenotypic correlation (r_p) as follows

$$r_p = h_x\, h_y\, r_a + e_x\, e_y\, r_e$$

r_p	=	phenotypic correlation
h_x	=	square root of the heritability of character x
h_y	=	square root of the heritability of character y
r_a	=	genetic correlation (of breeding values)
e_x	=	1- h_x
e_y	=	1- h_x
r_e	=	environmental correlation (includes non-additive genetic effects)

Equation II-13 : Phenotypic correlation as a function of genetic and environmental effects.

From the above it is clear that there are two major components that influence the phenotypic correlation, r_p of characters -

- low heritabilities of h^2_x and h^2_y that result in r_p being more dependent on r_e
- high heritabilities of h^2_x and h^2_y that result in r_p being more dependent on r_a

However, estimating r_a cannot be done from r_p alone, but instead, it must have some dependence on the amount of genetic variation *viz.* heritabilities. These genetic correlations r_a can be estimated empirically, in a similar manner to the heritability estimates of a single character. That is, the covariance estimates are partitioned into their respective sources of variation and the subsequent covariance of breeding values is estimated (Falconer, 1989). Essentially, these calculations are the same as for those described in the estimation of variance components of heritability values. However, the mean sum of cross products for two characters is used in place of the mean sum of squares (Hayward *et al.,* 1993). These simple correlations are provided by the *Pearson's correlation* option in SAS® and have varying degrees of freedom dependent on the correlation (between two characters) in question. That is, simple correlations only consider the two variables being correlated in the covariance analyses. In contrast, *Partial correlations* consider the effects of other variables simultaneously, when the two variables are being correlated (Snedecor and Cochran, 1967). These partial correlations are used in estimating r_a in the FMD study. These phenotypic (partial) correlations are slightly different from the simple correlations and have even lower degrees of freedom because of the nature of the MANOVA procedure in SAS®.

2. Genotypic correlations of vegetative characters

Extension of the classical Mendelian genetics from major (qualitative) gene models towards polygenic (quantitative) gene models has been described. As part of this, the earlier discovery by classical geneticists, that genes may have pleiotrophic effects has also been extended and utilised in quantitative genetics (Hallauer and Miranda, 1981).

Pleiotrophy is the phenomenon by which the same gene may affect several traits in a complementary fashion. In contrast, epistasis involves different genes affecting the same trait. The existence of pleiotrophic effects in quantitative characters is potentially very useful. For example, the case where two characters are affected by the same gene but one character has a high heritability and the other has a low heritability; this situation lends itself to the possibility of indirect selection. That is, selection of the highly heritable trait, could provide a correlated response in the other (lowly heritable) trait, provided their genetic correlation was reasonably high (Falconer, 1989; Hallauer and Miranda, 1981).

Genetic correlations are the correlations between the additive genetic variation (breeding values) of two characters, while the phenotypic (simple) correlations are a linear function of the genetic correlations, environmental correlations and heritability estimates (Equation II-13). Genetic correlations can be estimated in a similar manner to Equation II-12, by substituting the covariances of phenotypic values for their respective covariances of genetic (additive) values as estimated from the mean squares of cross products (MCP). Falconer (1989) reported that it is possible to have genetic and environmental correlations that are opposite in sign and very different in magnitude, although, the more usual case would be where both correlations are of the same sign and of similar magnitude.

Falconer (1989) suggested the reasons for large differences between r_a and r_e could be due to independent physiological pathways operating for each source (of genetic and environmental correlations). The r_a genetic correlations can be estimated when several characters are measured on the same individual, such as for the characters measured in the FMD study. The analysis of covariance is used in the GLM procedure of SAS® with the associated MANOVA statements. Subsequently, the same expectations used for the mean sum of squares of a single character (see EMS in Table I-2) are also used for the mean sum of cross products between two characters on the same individual.

Usually more than one character is measured on individuals (or plots of individuals) during the course of an experiment. These characters are chosen based on their significance to the breeding programme goals and objectives.

Generally, the plant breeder uses artificial selection (*herein known as selection*) to improve these characters. However, selection and improvement in a primary character may also have a correlated effect in another secondary (unselected) character. Falconer, (1989), defines this as the correlated response (*CR*) i.e. the expected response in character Y, when selection is applied to character X (Equation II-14).

$$CR_Y = i_x \, h_x \, h_y \, r_{Axy} \, \sigma_{Py}$$

CR_Y = expected response in *Y* from selecting *X*
i = selection intensity applied to character *X*
h_x = square root of the heritability of *X*
h_y = square root of the heritability of *Y*
r_{Axy} = genetic correlation of *X* and *Y* (of breeding values)
σ_{Py} = standard error of the phenotypic variation in *Y*

Equation II-14 : Correlated response of an unselected (secondary) character when a primary character is selected for (from Falconer, 1989)

Consequently selection for *X* can have either a positive, neutral or negative correlated effect on character *Y* (unselected). Clearly it is in the plant breeders interest to ascertain how these associations manifest and interact between the various key characters of interest, when selection is applied to a primary character. Hallauer and Miranda (1981) give an example of maize yield, which has low heritability of 0.18 and could be more effectively selected for by exerting selection pressure on a secondary trait such as kernel-row number which has a heritability of 0.57. However, the usefulness of this indirect selection procedure is dependent on the additive genetic correlation between these two characters, yield and kernel-row number.

Hallauer and Miranda (1981) reported a low to moderate r_a = 0.24 existed between these two characters. The correlated response for yield, by selecting for kernel-row number can be estimated and compared directly with the expected response by direct selection for yield. Comparing these two responses would quickly determine the best approach for advancing yield in maize. Hallauer and Miranda (1981) compared direct selection for yield and found it was more efficient than the indirect selection in this

instance. The relative efficiencies between various combinations of traits can also be estimated (assuming equal selection intensity is applied to both *X* and *Y* characters), with relative ease and is given by -

$$\frac{CR_x}{R_x} = \frac{i_y \, r_A \, h_Y}{i_x \, h_x}$$

$$= r_{A\,xy} \cdot \frac{h_Y}{h_x}$$

where $i_y = i_x$

CR_X	=	correlated response in *X* from selecting *Y*
R_X	=	direct response from selecting *X*
h_x	=	square root of the heritability of *X*
h_y	=	square root of the heritability of *Y*
r_{Axy}	=	genetic correlation of *X* and *Y* (of breeding values)
$i_{x/y}$	=	selection intensity applied to character *X* and *Y* ($i_x = i_y$ assumed to be equal)

Equation II-15 : Relative efficiencies of indirect and direct response between two characters (Falconer, 1989).

The relative efficiency of selection (RES) enables the plant breeder to decide the most effective method of individual selection for improving a single trait. The RES values that exceed 1.0 indicate the correlated response has some extra advantage. Conversely, RES values <1.0 indicate direct selection should be favoured. The plant breeder must decide at what point or threshold the RES information should be considered significant. Therefore, it can be seen that the utility of these genetic correlations is rather more potent than that of the phenotypic correlations. The simple phenotypic correlations are useful in a descriptive manner (retrospectively), while the genetic correlations are more robust and can be used more in a predictive manner. Accordingly, the estimated phenotypic and genetic correlations for the FMD study can be calculated empirically from these methods.

F. Selection strategies for improvement

In developing new cultivars it is important to determine the selection strategy that will optimise the response (*R*) to selection. Accordingly, different selection strategies have been developed for use under varying conditions. The single most important condition, however, being the relative amount of additive genetic variation available for selection pressure to be applied to (Borojevic, 1990). Selection of individuals, for use as parents, can be based on two sources of information. Firstly, individual phenotypic values can be used, although the ability of the phenotypic value to be transmitted to its offspring is dependent on the relative amount of additive genetic variation, alternatively, breeding values can be derived about the parents from a population of relatives (i.e. FMD study). Falconer (1989) defines the latter point as "information from relatives", such that -

$$P = P_f + P_w$$

where
P_f = deviations of family means from population mean.
P_w = deviations of individuals from family means.

In principle, however, there are two main selection methods - mass (phenotypic) selection and family selection (means based), all other types being variations or combinations of these two basic methods (Hallauer and Miranda, 1981). There are three selection strategies most commonly used in plant breeding work and they are

- **mass** (phenotypic) selection
- **family** (means based) selection
- **within** family selection

Each of these methods have been dealt with by Falconer (1989), and Kearsey and Pooni, (1996). However, a brief description of the various aspects involved in employing either of these selection strategies is as follows.

1. Mass (phenotypic) selection

Individuals are selected solely on their phenotypic value. It is the simplest method to operate and under certain conditions (high heritability) can yield a rapid response (R) to selection. In addition the term *"mass selection"* is used if the selections are collected together and crossed amongst each other i.e. *"en masse"*. However, if selected individuals are used as parents in a controlled manner, this is termed individual (phenotypic) selection (Kearsey and Pooni, 1996; Falconer, 1989). The efficacy of mass selection is most potent at heritabilities of 0.4 - 0.8 range.

2. Family selection

Under this selection strategy $P_f = 1$ for the between family deviations and $P_w = 0$ for the within family deviations (for their respective weightings). Families of either full or half sib relationships are selected according to their family means. Conditions, which favour this strategy, are

- characters with low heritability values
- little variation due to common environment
- relatively large family sizes.

Therefore, low heritable characters allow the individual variations of phenotypes to cancel each other out, at which point the family mean becomes a good estimator of the genotypic mean. Conversely, any environmental deviations common to members in families can impair the usefulness of family selection, by swamping genetic differences between families. There are a number of difficulties in applying family selection methods. Consideration must be given to the effects of inbreeding, particularly, in the case of kiwifruit, because the use of hermaphrodites in some selfing populations has been shown to have negative effects for plant vigour and increased mortality of seedlings (McNeilage, 1997). Additionally, large family numbers and family sizes must be used in order to avoid these inbreeding effects, and therefore, family selections would be very costly of space and resource in its application to the kiwifruit breeding programme. Although the example above is for an extreme level of inbreeding, caution must still be exercised when recurrent selection procedures are employed, even at the full-sib level.

a) Sib selection

Some characters may not be measured on particular individuals; for example, in kiwifruit the fruiting characteristics of male plants cannot be measured. If these individuals are to be used as parents, they must be selected on the performance of their relatives. This amounts to family selection, although, the parental selections themselves do not contribute to the family mean. Falconer (1989) defines this as sib selection, and its distinction from family selection is dependent on family size and its response (R). The use of sib selection in kiwifruit can be applied to selection of males in progeny families for the fruiting aspects of their female F_1 siblings i.e. female fruiting character mean values.

b) Progeny testing

This procedure involves half-sib relatives, and selection of the individual parent is based on the performance of its progenies. The mean value of an individual's offspring is the practical definition of it's breeding value (see earlier discussion). Essentially then, the first part of progeny test evaluation, is in fact, family selection. However, the problem with this strategy, is the fact that the parents cannot be selected until their offspring's performance are evaluated. In addition, the offspring themselves may also be selected as parents, this can lead to some confusion with different generations being selected as parents and crossed. Evidently, progeny tests differ from family selection at the point where the selected families (i.e. respective parents) are allowed to go on breeding, with an increased family size. Therefore an increased selection intensity can be used without the danger of inbreeding (Falconer, 1989), although, it is in fact sib selection at this stage, and it too will suffer from the need for large space requirements. Several examples of this type of 'male progeny testing' have been successfully used in animal breeding. Indirect selection for bulls (used as sires) and their effects on milk fat and protein yields in the dairy industry have led to the development of an indexing system for these sire bulls (Dekkers, 1994). Information gained about the effects of the male (staminate) kiwifruit parents on various characters can only lead to an improved selection response. If only female parents are selected then genetic gain is only half as effective as compared to selecting for both male and female parents (Beatson, 1991).

3. Within family selection

The best individuals from each family are selected as parents, and in contrast to family selection, the weightings for $P_f = 0$ and $P_w = 1$, respectively. In addition, the replacement of parents, based on all families, ensures a lower level of inbreeding is maintained (compared to family selection). Therefore, the conditions that favour the use of *within family* selection are

- when the component of variation due to common environment is significantly large (i.e. low heritability)
- where space is limited, within family selection optimises its use of breeding space
- effective population size is doubled (due to the replacement of parents based on families)

4. Comparing response to selection strategies

From the selection strategies above, it can be seen that certain strategies are more suited to particular circumstances. These different circumstances are dependent on the amount and type of genetic variation present for the character being selected and their family size. However, Falconer (1989) used the following equations (below) for comparing these two selection strategies. From these equations, the selection strategy that maximises response for certain fruit characters can be identified.

- Individual selection $R_i = \mathrm{i}.\sigma_{\mathrm{P}}\, h^2_n$
- Family selection $R_f = R_i * [\{1+(\mathrm{n}-1)\mathrm{r}\}/\sqrt{\{\mathrm{n}(1+(\mathrm{n}-1)\mathrm{t})\}}]$

The FMD study will only be concerned with *individual* selection strategies and in addition only its responses in selected fruit characteristics will be reported here. The reason for this, is partly due to the problems with sexual dioecy in the 1996 FMD fruit data, leading to these genetic estimates being less reliable than those based on later years from more sexually mature vines (with a higher number female or fruiting vines). Therefore, investigating response to other selection strategies is best left for those genetical estimates that will be based on later year's data (1997 and 1998).

III. Materials and Methods

The Factorial Mating design (FMD) study had over 3,000 plants monitored in two randomised complete block (RCB) factorial designs for various vegetative and fruiting characters. Vegetative characters were measured on all individuals in both factorials. These included annual trunk diameter and number of prominent (swollen) buds per 500 mm cane i.e. vigour measurements. Seedlings that were sexually mature in 1995 also had their juvenile period, flowering range and median flowering dates recorded (floral measurements). Nineteen fruit characters were collected during the 1996 fruit season from 430 female vines whose crop load was ten or more fruit. These data are categorised into three main assessments, pre-harvest, harvest and post-harvest (see list on page 67). The objective of these measurements were to estimate the following genetical statistics pertaining to the 1991 *Actinidia deliciosa* germplasm,

- heritabilities (both narrow and dominance) and their standard errors
- general and specific combining abilities of the parents i.e. breeding value
- phenotypic and genetic correlation's amongst vegetative and fruiting characters

These data could be used to identify if any moderate to high *genetic* correlation's existed between vegetative and fruiting (sexually mature) characters. This was the main reason for measuring trunk diameters over the four-year period (1993-96). Genetic correlation's between these trunk diameters, from sexually immature seedlings compared with their floral/fruiting stage, i.e. at sexual maturity, could prove to be very useful as an early indirect selection tool for kiwifruit plant breeding.

A. Experimental design

Several individuals were randomly selected, for use as parents, from the 1991 *Actinidia deliciosa* germplasm and were crossed in a factorial scheme to produce a large number of full sib families (FS). The project is divided into two distinct crossing experiments.

- *Factorial One* - which has 49 full sib families, from 7 females crossed to 7 males
- *Factorial Two* - which has 42 full sib families, from 6 females crossed to 7 males

Two reference populations an 'early' [*Factorial One*] and 'late' [*Factorial Two*] sets of sub-populations were then formed. The reason for separating these two sub-populations was because of their inherent differences between each other for flowering times and fruit maturity. These differences will become more evident later (Chapter 4). These full sib families or bi-parentals (BiPs) have been assigned alphanumeric codes as indicated by a combined letter (A-N for their respective female parents) and number (1-15 for their respective male parents). The summary of actual vine numbers and their codes of full sibs in each factorial are detailed in the following tables.

Table III-1 : Summary of parental arrays and full sib families in Factorial One

Factorial One	Bi-parental combinations and number of vines per Family							
				Male				**sub -**
Female	**01**	**02**	**06**	**07**	**09**	**12**	**13**	**totals**
A	36	36	36	36	36	36	36	*252*
B	36	36	36	35	35	**7**	36	*221*
C	36	36	36	36	36	36	36	*252*
D	35	35	36	**1**	36	35	35	*213*
E	36	**14**	36	36	36	36	36	*230*
H	35	29	33	32	35	30	36	*230*
M	35	36	36	36	36	36	35	*250*
sub - totals	*249*	*222*	*249*	*212*	*250*	*216*	*250*	*1648*

Key: BiP combination *M02 =36* progeny per BiP family. *Half-sib sub-totals* - if a complete set of plants is present (36 per treatment) then 252 should be the sub-total by females and males, (numbers in **BOLD**, are where some plots are missing); see accession codes alphanumeric BiP list in appendix A.

Table III-2 : Summary of parental arrays and full sib families in Factorial Two

Factorial Two	Bi-parental combinations and number of vines per Family							
				Male				**sub -**
Female	**03**	**04**	**05**	**08**	**11**	**14**	**15**	**totals**
F	36	35	36	33	32	35	35	*242*
I	36	36	36	36	35	36	35	*250*
J	36	35	36	36	36	36	35	*250*
K	35	34	36	33	34	36	**17**	***225***
M	36	34	34	36	35	35	34	*244*
N	35	36	35	36	36	34	36	*248*
sub - totals	*214*	*210*	*213*	*210*	*208*	*212*	***192***	*1459*

Key: BiP combination *M02 =36* progeny per BiP family. *Half-sib sub-totals* - if a complete set of plants is present (36 per treatment) then 252 should be the sub-total by females and males, (numbers in **BOLD**, are where some plots are missing); see accession codes alphanumeric BiP list in appendix A.

The target number of progeny per family was 36 individual seedlings and this was achieved in most cases. There were four bi-parental families that did not produce sufficient numbers of seedlings for complete external replication (i.e. whole-plots missing), these families are B12, D07 and E02 in Factorial One; and K15 in Factorial Two. Other families had missing plants at the replication level, but this imbalance is minor in comparison. The effective analysis of a two-way classification depends heavily on complete cells (i.e. full sibs or treatments), consequently, the experimental design has been compromised by the imbalance. If these cells are absent or incomplete, then the information derived from them may be biased (Steel and Torrie, 1981).

The physical layout of the two randomised complete block (RCB) designs are given in Appendix *B*: Figure V-1. Each factorial has 6 complete blocks of 3 rows each, each 'block' containing a complete list of treatments (family combination) or plot. Each plot has 6 full sib plants or internal segregates per plot (see Appendix *B*: Figure V-1 and V-3). The general overview in Appendix *B*: Figure V-2 shows the orchard layout of the RCB designs in relation to each other. The failure of some BiP's has effected how the data will be analysed; these issues will be discussed in the next section on statistical design.

1. Statistical design and analyses

a) Inference Base of the Factorial Mating Design Study

The parents used in the two factorial mating designs were mostly a random selection from the complete range of the *Actinidia deliciosa* 1991 germplasm available in New Zealand. They were assumed to be a small but representative sample of the *A. deliciosa* accessions in the New Zealand Kiwifruit Breeding programme (NZKBP). The inference base population (IBP) is, therefore, considered to be the available gene pool within the 1991 New Zealand kiwifruit *Actinidia deliciosa* breeding programme. The purpose of the FMD study is to estimate genetical information for several traits of interest in the IBP, based on these sample accessions (parents). Sampling effects of those individuals used as parents could be a source of bias in the estimation of heritabilities. Clearly, it is important to define the reference populations from which these data are derived. The relatedness of most of the parents from the inference base population is largely unknown. A few parents are known to be related (as half or full sib) but for the purpose of the FMD study the level of inbreeding will be set to zero.

Results from the FMD will pertain solely to the New Zealand germplasm (as at 1991) and in particular only to those accessions sampled in the FMD study. Although, the random effects model II (see below) used in the analysis of variance is based on the inference base populations (IBP), this forms the '*universe*' from which an infinite population of treatment effects will pertain to. Therefore any inferences made about the New Zealand *A.deliciosa* germplasm are expected to be valid, within the confines of plant selection being improved from these sources. Furthermore, any extrapolation from the IBP to the *Actinidia deliciosa* species should be avoided, given the small number of genotypes sampled (as parents) and the accessions used were not a representative systematic sample of the species from China. The FMD study data is derived from a single season (one environment) and from young fruiting vines, the majority of which are in their first fruiting season, therefore, these results should be considered tentative at best.

(1) Single season environment

Selection of superior genotypes is generally made with reference to a particular class or population of environments. These environments can be broadly classified as macroenvironments or growing areas/regions (Nyquist, 1991). Each macroenvironment has nested within itself an infinite number of microenvironments, which include all factors that influence the phenotype of an individual except for its genotype. Nyquist (1991) suggested there was greater variation *within* macroenvironments than *between* macroenvironments. The environment universe about which inferences are to be made must be (clearly) defined.

The information collected during flowering 1995 and fruiting 1996 forms the basis of the '*single season environment*' or simply referred to herein as the **1996 fruit season**, about which genetical estimates apply. The sample of time (inter-year effect) cannot be separated from the treatment effects (total genetic variation) in this study because there is no provision in the model for the 'time' (year's) effect. However, by employing a different model with a pooling of years in a split plot design the 'time' effect can be separated from the total genetic variance but this is beyond the scope of the present study.

Data from the 1996 fruit season will, therefore, include the genotype environment interaction effect (GxE) as part of the total genetic variance. The specific environment used in estimating genetical statistics from the FMD study is defined as

- the growing area at the Te Puke Research Centre is considered the macroenvironment
- a time effect (years), considered to be a random effect
- climatic conditions in 1995/96 season are also considered to be a random effect

Searle (1971) suggested that the 'time' effect (i.e. years) could be considered as either a fixed or random effect. It can be considered fixed because it is not a random sampling of time nodes. Also it can be considered random, as for example in yield, where the character itself inherently responds differently over time. Therefore, time was considered a random effect in the FMD model for this reason. This also simplifies the subsequent expected mean squares i.e. E(MS).

In summary, the single season environment (or 1996 fruit season) data suffers from three major limitations

- single year phenotypic values may contain a bias due to sampling only one time node (Hansche *et al.,* 1972 and 1972a)
- no estimate available for the genetic fraction of the within plot variance in the 1996 fruit season
- GxE interaction effect (if present) is included in the residual error term; also if this source of variation is significantly large then there will also be a bias in the genetic estimates

Gordon (1979) discussed various issues regarding the suitability of perennial data collected serially over time, suggesting that effects from different times may not be independent (i.e. carry over of physiological effects) and that this violates the assumption of no covariance leading to a bias in the variance component estimate. The single season sampling (although considered a random effect) contains a bias simply due to selecting the 1996 fruiting season. Furthermore, serial data that is collected from 1997 and 1998 also contain bias for the same reason (Nyquist, 1991).

(2) Random effects model II

The expected mean squares (EMS) table is based on the random effects model II (Steel and Torrie, 1981). The random effects model states treatment (full sib) effects ($t_{i's}$) are a random unbiased sample of $t_{i's}$ from a infinite population of possible treatment (full sib) effects, within our base inference universe. Therefore, inferences are made about the population of treatment effects, as indicated from the sample statistics (Steel and Torrie 1981). The FMD study conforms to this basic assumption, with the random selection of parents crossed in full sib combinations (or treatments), represents the sample of $t_{i's}$. The inference base population (IBP), described above, forms the population of $t_{i's}$ about which inferences are to be made.

The analysis of the FMD data sets uses the Type II sum of squares (*step down partials*) in the GLM procedure of SAS®. The Type II SS method has the restriction of not adjusting for the interaction effect when estimating the main effects sum of squares (Littell *et al.,* 1991). Although, the Type II SS estimates the interaction term $\alpha\beta$ in a different way to either Type II or IV SS, it still *declares* the interaction effect significant, whenever Type III or IV SS *declares* the interaction significant. However, in the latter cases (Type III or IV SS) were always more conservative. The suitability of Type II SS method was demonstrated by comparing the empirical results of Type II SS *step down partials* and Type III SS *partial* method for these data. The most convincing evidence was that the Type II SS *step down partials* were very close to Type III and IV SS *partial* methods, even in the presence of a significant $\alpha\beta$ interaction effect (data not shown).

The FMD experimental design is based on the randomised complete block (RCB) design, where by definition, the '*blocks*' or replications are random effects. The segregates of plants (≈ internal replications) were grouped into full sib plants of similar size; this ensured all plants in each external replicate (or plot) were as alike as possible. Grouping plants in this manner augments the blocking effect (Steel and Torrie, 1980). In addition, the collection of subjective data, such as flowering percentage assessments, was done with each assessor being assigned to specific 'blocks' or replicates. The reason for this was to 'block' for the differences (if any) between the various assessors observations.

B. Problem of data imbalance

The **General Linear Model** (GLM) procedure in SAS® is best suited for the analysis of unbalanced data. In general, unbalanced data in a two-way structure (FMD) suffer from the confounding of differences *between* factor (A) means, e.g. female 1 - female 2 effects, by effects of other factors (B) e.g. male effects (Littell *et al.,* 1991). An important distinction in the case of a balanced design i.e. with complete replication, versus the FMD study, is that the expected mean squares are orthogonal, thereby allowing unbiased estimates of variance components to be calculated (Steel & Torrie, 1980).

The GLM procedure should be used whenever there are unequal numbers of observations in any specified model class variable. An example of this occurs in the *whole-plot* level specified in the EMS-table (Table III-5) of the FMD study.

There were supposedly 6 plants that could have been measured in every plot, in practice however, the actual plant numbers measured varied from 0 to 6 per plot for certain full sib treatments. Tables V-4 and V-5, in appendix *A*, illustrate the number of plants *actually* measured in each plot for the vegetative and fruiting characters, in the 1996 season for Factorial One and Two respectively. It is evident from these tables that the imbalance at the plot level (external replication) is moderate in Factorial One, while having less of an effect in Factorial Two, especially with regard to the fruiting characters.

Analyses of each complete factorial data set is also compromised by the fact that, in at least some treatment (full sibs) cases, the number of plants at the plot level was zero, (see Appendix *A*: Tables V-4 & Table V-5). Consequently, a reduced number of full sib combinations was analysed, in order to improve the level of imbalance at the whole plot level. In addition, there were different reduced FMD data sets used in each Factorial separately, for their vegetative and fruiting characters. In general, the level of imbalance has been more severe for fruiting characters than for vegetative characters. This can be seen by the harmonic mean plant number measured per plot in the fruiting data, which ranged from 1.59 to 2.48 compared with the vegetative harmonic mean plant number measured per plot data, that ranged were between 3.89 to 5.91 (data not shown).

1. Reduced FMD approach for vegetative data

The following design reductions for each factorial was used in order to improve the imbalance at the whole plot level. This resulted in the mean (harmonic) plant numbers per plot varying from 3.89 to 5.91 across both data sets for the ten vegetative characters.

Full FMD Specified		**Reduced FMD Specified**
Factorial One 7 x 7	*vs*	Factorial One 5 x 5 (A,B,C,H & M **x** 01, 06, 07, 09 & 13)
Factorial Two 6 x 7	vs	Factorial Two 6 x 6 (F,I,J,K,M & N **x** 03, 04, 05, 08 & 11)

Therefore, Factorial One was analysed as a "reduced FMD of 5 x 5" design (also referred to as F1 v 5x5) and Factorial Two as a "reduced FMD of 6 x 6" design (also referred to as F2 v 6x6) for the vegetative characters. These reduced designs are expected to alleviate some of the imbalance problem, in estimating unbiased variance components.

2. Reduced FMD approach for fruiting data

The problem of imbalance is greater in the fruiting data than it was in the vegetative data, and there are several reasons for this, as discussed in the following sections. Generally, the major cause of the imbalance is due to the unknown sex of the seedlings at the time of *field planting*. Consequently, the female seedlings distribution amongst the plots is completely at random and as such is expected to follow a binomial distribution because of the (possible) nature of sex determination in *A.deliciosa* species i.e. 1:1 sex ratio (Testolin *et al.*, 1995, McNeilage, 1997).

a) Sex at flowering – male or female

Actinidia is functionally dioecious; consequently, at sexual maturity (and ignoring sexual variants like fruiting males) plants can be strictly classified as male or female. The female to male ratio could approach 1:1 by full maturity, i.e. when all plants are flowering. At the time of this study, 68% of all seedlings were sexually mature, with a 1:1.32 female to male ratio i.e. there were 32% more male plants compared to female plants at flowering 1995; resulting in almost 900 females across the two factorial designs. If the assumption of a female to male ratio of 1:1 (at full sexual maturity) is correct, then

there could be a further 670 immature females. From this assumption, only 57% of the expected females have flowered so far. Clearly, this may not the most informative data set to test the characteristics of fruiting attributes; considering 43% of the females (expected) have not yet flowered. The random physical distribution of these 900 females across the plots represents another problem of imbalance in the fruiting data.

b) Female plants distributions

Because the sex of the seedlings was unknown at the time of planting and a randomised complete block (RCB) planting design was used it is reasonable to assume the plants from each BiP were randomly planted. Consequently, seven combinations of male and female plants were possible at the whole plot level i.e. amongst the six segregates. Sexually mature vines can be nominally categorised as either male or female at sexual maturity. This results in a seedling being sexed as female or male with the probability of ½. The probability of a specified number of females (or males) flowering in each plot can then be estimated by using the binomial distribution theory (Snedecor and Cochran, 1967). The following Table III-3 illustrates the binomial expectations for a specified number of females (or males) occurring, by chance events, in a plot of six plants at full sexual maturity. The 1995 flowering data *chi-square* tests were significant in both sets therefore rejecting the null hypothesis that the *expected* versus *observed* plot numbers per class followed the binomial distribution with a probability of $p = ½$. Three major factors were considered important in influencing the distribution of female vines (and their fruiting data) in the experiment and these include

- random distribution of female plants within families - due to sampling variation when seeds were extracted and germinated
- random distribution of female plants during planting - because of the unknown sex of seedlings
- level of sexual maturity in 1996, causing the ratio of females to males to have a male bias - (skewed) especially when sexual maturity of the population is low to moderate

These three factors (above) had a major impact on the fruiting attributes in this study because of their effects on the external replicate imbalance.

From Table III-3, an estimated 21% and 17% of all plots in Factorial One and Two respectively, did not have any fruiting data collected during the 1996 fruiting season. This type of imbalance at the external replicate (or plot level) has serious implications in the two-factor RCB analyses of the fruiting data. The reduced design analysis was used in order to try and redress these issues.

Table III-3 :Probability of a specified number of female (or male) vines flowering in a plot; also their expected and observed plot totals (with the specified genders) in each class.

		Factorial			
		One		Two	
Number of females per class	**Prob.**	**Observed 1995 (1996)**	**Plot no. expected**	**Observed 1995 (1996)**	**Plot no. expected**
0	*0.01563*	**57** ***(5)***	4.298	**41** ***(11)*** [1]	3.845
1	*0.09378*	**83** ***(45)*** [1]	25.789	**69** ***(30)*** [1]	23.070
2	*0.23445*	**73** ***(61)***	64.474	**64** ***(69)***	57.675
3	*0.31260*	**42** ***(75)***	85.965	**48** ***(75)***	76.899
4	*0.23445*	**17** ***(62)***	64.474	**16** ***(40)***	57.675
5	*0.09378*	**1** ***(22)***	25.789	**6** ***(19)***	23.070
6	*0.01563*	**2** ***(5)***	4.298	**2** ***(2)***	3.845
Totals	***1.00032***	**275***	**275.087**	**246***	**246.079**
Pr(χ2)		**0.00 (0.90)** [2]		**0.00 (0.75)** [2]	

* - These observed values are only from total plots with four or more plants; The *chi-square* test reveals the lack of fit of the observed values with the binomial distributions; for the 1995 flowering season.
[1]Ignoring the most divergent classes in **1** - Factorial One and classes **0** and **1** in Factorial Two for their 1996 females
[2]The *chi-square* test for 1996 flowering season (with ~90% sexual mature)

c) Optimum plot size for female distribution

Assuming a binomial distribution of females per plot, the expected number of plots with no female vines is approximately four in both Factorial designs (Table III-3). The chi-square test for the 1995 flowering season reveals the lack of fit for the 1:1 sex ratio. The chi-squared probabilities of zero in both cases, show the expected 1:1 ratio is not followed for the 1995 flowering season (with 68% vines sexual maturity). In contrast, almost 90% of the vines had reached sexual maturity by the 1996 flowering season (see Appendix *A*: Table V-1). From these data it can be seen that the observed numbers of

plots *without* females was 5 plots and 11 plots for Factorial One and Two respectively (data in brackets in Table III-3). Therefore the increased sexual maturity in the population has shown a trend towards the binomial expectations. The overall *chi-square* probability was still low for the 1996 flowering, largely due to the most divergent females per class, i.e. in Factorial One **class 1** and **classes 0** and **1** in Factorial Two. However, if we ignore these most divergent classes, the distribution does approximate the binomial (Pr > 0.90 and >0.75 respectively). Therefore it is possible that when the whole population is sexually mature (100%), that the overall chi-squared probability could tend towards accepting the expected sex ratio of 1:1. Accordingly, the initial planning of the experimental design could have tested the various plot sizes using this binomial theory. For example, increasing the plot size to nine, but remaining within the constraints of the total resources used, would give the expected female distributions as in Table III-4.

Table III-4 : Expected plot numbers of a binomial distribution having specific female (or male) classes and a plot size of nine.

Number of females per class	Prob.	Factorial One Plot no. observed	Factorial Two Plot no. observed
0	*0.00195*	0.3822	0.3276
1	*0.01758*	3.4457	2.9534
2	*0.07031*	13.7808	11.8121
3	*0.16406*	32.1558	27.5621
4	*0.24609*	48.2336	41.3431
5	*0.24609*	48.2336	41.3431
6	*0.16406*	32.1558	27.5621
7	*0.07031*	13.7808	11.8121
8	*0.01758*	3.4457	2.9534
9	*0.00195*	0.3822	0.3276
Totals	***0.99998***	**195.997**	**167.9966**

* - the observed values are only from total plots with four or more plants; The binomial distribution over the nine plots illustrates the effect of almost no plots with zero (class 0 or 9) female or male vines.

These expected female numbers per plot (in Table III-4) were calculated using the following assumptions

- female (and male) vines follow a binomial distribution pattern
- an increase in the plot size from 6 to 9 with no change in the total resources
- a reduction in block (rep) numbers from 6 to 4
- a reduction in total plot numbers from 294 to 196 in Factorial One and from 252 to 168 in Factorial Two due to increased plot size

The probability of '*no females per plot*' has been reduced from 4 to 0.5 (approx.), simply by increasing the plot size. The immaturity of the populations and the tendency for more males to flower sooner severely comprises the 1996 FMD fruiting data due to the increased external replicate imbalance. Better planning in the earlier stages could have alleviated this problem to a certain extent. It is expected that the fruiting data analyses and imbalance problems will have a lesser impact when the populations have reached full sexual maturity. Several factors influence the type of analyses possible with the fruiting data as discussed above. The plant segregates imbalance due to the distribution of females, has complicated the fruiting data analyses, resulting a reduced FMD approach being used. In a similar fashion to the vegetative data, the following reduced designs were employed in an attempt to redress some the difficulties of the data imbalance.

Full FMD Specified		**Reduced FMD Specified**
Factorial One 7 x 7	*vs*	Factorial One 3 x 7 (C, H & M x 01, 02, 06, 07, 09, 12 & 13)
Factorial Two 6 x 7	*vs*	Factorial Two 3 x 4 (I, M & N x 03, 05, 08 & 11)

Therefore, Factorial One was analysed as a "reduced FMD of 3 x 7" design (also referred to as F1 f 3x7) and Factorial Two as a "reduced FMD of 3 x 4" design (also referred to as F2 f 3x4) for the fruiting characters.

3. Advantages of the reduced FMD approach

The two main reasons for utilising this reduced FMD approach include

- minimising the imbalance at the external replication level
- providing a "reliable" data set with sufficient information to base statistical estimates and subsequent genetical interpretation

Furthermore, the expected degrees of freedom in the analyses as listed in the expectations of means squares EMS-Table III-5, can only be achieved when the reduced designs are employed. In contrast, any analysis using the complete data sets severely reduces the degrees of freedom for their respective sources of variation because of the imbalance. Partitioning these original sums of squares, into their respective variance components, by using the incorrect degrees of freedom clearly invalidates any significance tests. Therefore, I have chosen to trade off the "universe representation" (by reducing the design analyses) in favour of increasing the reliability of the analyses.

4. Limitations of using reduced FMD

The disadvantage with these reduced design analyses, is that less representatives from the IBP are sampled; subsequently a new source of bias is introduced. In the case of the reduced Factorial One 5 x 5 design (10 parents), four less parental genotypes are sampled as compared to the full 7 x 7 design (14 parents). However, I do not consider this a serious bias in its representative ability, because the reduced FMD analyses samples 10 out of the 14 (i.e. 72%) parental genotypes. More importantly, in my opinion, the information derived from these 72% is of a more reliable nature compared to the information derived from the full FMD analyses. The use of the reduced FMD analyses does not alleviate the internal replication imbalance but the imbalance is less noticeable with these reduced FMD analyses than compared with the full design analyses. In comparing both the full and reduced FMD analyses, there is a loss of some information involved by the use of either method. However, genetical estimates based on *fewer* parental genotypes while ensuring data with the *least* level of imbalance are used, as in the reduced designs, are considered more 'reliable' in my opinion.

C. Vegetative and fruiting characters

1. Plant characteristics

Vegetative traits and their respective data collection methods are listed below. All data, excluding 3 of the 4 annual trunk diameters, were collected during August to December of 1995; that is, they represent flowering and vigour measurements in a single season. The other 3 annual trunk diameter measurements, (1993, 1994, and 1996) were also analysed and used to investigate correlation's between these and their vigour and flowering characters from the 1995 flowering season. In addition, summary details for each factorial for 1995 and 1996 sexual maturities and ratio information is also included in Appendix *A*: Table V-1.

Vegetative data recorded

Trunk diameter records (August 1993/4/5/6).
The individual trunk diameters were measured annually, at 20 cm from ground level using Sylvac® digital calipers. The measurements, in millimeters (mm), were taken during the last week of August in each of the years 1993, 1994, 1995 and 1996.The cumulative trunk diameter, CU96, represents the sum of the incremental trunk diameter changes between each successive year from MM93 to MM96. The vine growth rate (AGR) is also calculated by transforming the **non-linear** plant growth as change in trunk diameter [numerator] over the change in time series [denominator].
i.e. AGR = [log(MM96)-log(MM93)] **/** [3] (from Hunt, 1982) i.e. the log (base10),

attribute code : [**MM93, MM94, MM95, MM96, CU96, AGR**]
scale : millimeters (mm)

Prominent buds recorded (September 1995).
Subjective assessments were made on dormant winter buds as either having the potential to become vegetative shoots in the new season's spring growth or not producing shoots at all. The former were counted as 'prominent buds' (prominent in height and large in diameter) while those buds that were flat (in height) and small in diameter (size) were not. The number of prominent buds was counted from the basal end of the cane out to 500 mm towards the terminal end of the cane. (i.e. number of prominent buds/500 mm).Two canes were sampled (one cane from each side of the vine) and an average PRBD value calculated per seedling.

attribute code : [**PRBD**]
scale : No. of buds. (No.= number)

Flowering data recorded

Median flowering

Data was collected as subjective percentage assessments, of flowers open on set dates. The vines were assessed every Monday, Wednesday and Friday (weather permitting) during November to December of 1996.. These "days" were given a value as based on their interval from an arbitrary point, **1st November 1995** as **Day 1** i.e. **datum value**. Each assessment date was then assigned their respective numbers of days from a datum (start) point, and their observed "percentage flowering" data were weighted by their respective "day" values and summing across their flowering range (see next character). Resulting in a estimated median "day" that represents that point at which 50 % of the 'weighted' flowering data was completed. It is important to note that this does not represent when the vines were at 50 % full bloom, but simply indicates the median point in days from the reference datum.

attribute code : [**MEDF**]
scale : No. days from datum (Nov. 1, 1995) to median flowering day

Notes: The assessors' subjective percentage flowering estimates are open to extreme variation, and in an attempt to minimise these effects, particular assessors were assigned to specific replicated 'blocks' therefore minimising the error within blocks and providing local error control by the blocking effect.

Flowering range

The flowering period was measured as the interval (in numbers of days) between 0% flowering and 100% flowering. The 0% observation was nominated as the date preceding the first flowering being recorded, while the first observation recorded as 100% was taken to indicate the end of flowering.
attribute code : [**FRNG**]
scale : No. days from 0% to 100% flowered

Gender and sexual maturities

The number of female and male vines in the population at the 1995 flowering was used to represent the sex ratios of the various full sib families. The female to male ratio of sexually mature populations is known to approach 1:1 (Testolin *et al.*, 1995). The nominal categories male, female or immature were taken as strict sexes i.e. each flowering vine was classed as either male, female or immature, irrespective of the possible, but rare, occurrence of fruiting males or hermaphrodites in the population.

attribute code : [**GEND**]
scale : No.

Juvenile period

The juvenile period was measured as *years-to-flowering*: from when the plants were *first planted* in the field up to when they *first flowered.* Each plant was measured from their time of planting to their sexual maturity at November 1995. The number of *years-to-flowering* by November 1995 ranged from 1-3. Thus the family mean represents a decimal fraction for the average of its progenies juvenile period.

attribute code : [**JVPD**]
scale : Years

2. Fruiting characteristics

There were nineteen fruiting characters measured in both factorials (reduced designs). Although there are almost 900 female vines (in total) across the full FMD, less than 40% of these vines had sufficient fruit numbers per vine (>10 fruit), available for the 1996 fruiting data set to be completed. Consequently, the total number of vines available for testing was much less than expected. The methodologies used with each of the three main assessment categories (Pre-harvest, harvest and post-harvest) are outlined as follows.

Fruiting data recorded

Pre-harvest assessments

Fruit number per vine

Fruit number per vine was counted during March 1996, preceding the start of the fruit data collection. This was done in order to identify those vines with less than ten fruit and those with greater than ten fruit; this allowed for the planning of further assessments (see harvest procedures). In addition, fruit number per vine was used as a precocity indicator.

attribute code : [**FNO**]
scale : No. per vine

Screening data for maturity

Maturity testing of large populations of genotypes is a difficult process. During the 1996 fruit season, all vines with ten or more fruit were monitored on three pre-determined dates (17th April, 6th May and 21st May, 1996); with the screening dates resulting in early (E), mid (M) and late (L) samplings respectively. From each of these (three) screening dates, a sub-sample of (up to) three fruit per vine was taken and their dry matter (EDM, MDM and LDM) and soluble solids concentration (EBX, MBX and LBX) were recorded. The objective of the screening technique was to ensure a threshold level of 8% soluble solids concentration %SSC (or higher) was reached *on-vine* - before the harvesting of each vine.

Notes: The threshold level 8%SSC was considered an optimal %SSC to ensure the fruit were close to their full physiological maturity. By the 21st of May, almost 86% of all vines (with ten or more fruit) were harvested. The remaining vines whose fruit were not over the threshold (8%SSC) were left on the vines and harvested irrespective of their %SSC, on the 31st May 1996. Consequently, there were three screening dates (with data collected) and the fourth date was a compulsory strip harvest (31st May 1996). The following table summaries the number of screening dates, number of vines harvested and the type of data (variables) collected.

Summary of dates and vine numbers for screening data		
Screening	Number of vines ≥ 8% SSC	Data collected
17 April	150	EBX, EDM
6 May	246	MBX, MDM
21 May	78	LBX, LDM
31 May	77*	compulsory harvest
Total	551	*(vines ≤ 8% SSC)

EBX = early brix (%SSC), EDM= early dry matter (%DM)

MBX = mid brix (%SSC), MDM= mid dry matter (%DM)

LBX = late brix (%SSC), LDM= late dry matter (%DM)

*attribute code:***[EBX; EDM; MBX; MDM; LBX; LDM]**
scale : %SSC for Brix and %DM for dry matter

Harvest assessments

Yield

Fruit were harvested from each vine once the threshold of 8%SSC or higher was reached. The harvest dates usually followed the screening dates by 1-3 days (later) and were, 24th April, 9th May, 23rd May and 31st May 1996. Almost 80% of all fruiting vines (that had ten fruit or more) had been harvested by the 21st of May 1996. Total fruit weight (kg) of each vine, at harvest, was recorded in the field using an Avery® (analog) spring-loaded scale. The harvest yield data was then added to the fruit weight data collected from the successive screening dates, to give the total yield (YLD) for 1996.

*attribute code:***[YLD]**
scale : kg

Harvest data

A random sub-sample of up to 30 fruit was taken from the harvest yield and weighed using a single decimal place Mettler ® electronic balance (± 0.1 grams). These data provided a representative estimate of the mean fruit weight for each vine (FWT). A further sub-sample of 6 fruit was taken from the original 30 fruit sample; these were used for the harvest measurements (3 fruit) and sensory assessments (3 fruit), with the remaining fruit used for storage assessments (with up to a maximum of 15 fruit used for storage). Data collected from the three fruit sub-sample at harvest included, % dry matter (HVDM) and % soluble solids (HVBX).

*attribute code:***[HVDM; FWT; and HVBX]**
scale : %DM, gms and %SSC

Post harvest assessments

Generally, fruit shape is uniform within a single genotype, provided the fruit are well pollinated and growth is unimpeded. Two shape descriptors were recorded, the first method was the **L:D** descriptor (from Beatson, 1991) which is the ratio of the length to its average diameter ratio. The second method used the visual image processing (**VIPs**) software to capture the outline of the fruit. Graphic-capturing hardware was used to take a series of percentile measurements down the central axis of the fruit. The shape measurements were taken on a single fruit in each method **L:D** and **VIPs**. The 'single (average) fruit' was chosen from the 30 fruit sub-sample as being a typical fruit (for shape) and for being closest to its mean fruit weight.

L:D shape descriptor

The following measurements were taken on an 'single (average) fruit' from each vine, using a Sylvac® digital calipers in millimeters (mm's); the same fruit was then measured using the VIPs shape descriptor (see below).

length		=	from calyx (stem) end to stylar (blossom) point end(*LENM*)
diameter	maximum	=	diameter at equatorial center of *maximum* profile(*DMAXM*)
diameter	minimum	=	diameter at equatorial center of *minimum* profile(*DMINM*)

attribute code: **[LENM; DMAXM; DMINM]**
scale : all in millimeters (mm)

VIPs *shape descriptor*

The same fruit that was measured for the L:D shape descriptor was also measured in the VIP's methodology as follows. Each fruit was placed on top of a specially designed prong with its calyx end pointing downwards and with its flatter (DMAXM) profile positioned perpendicular to the video camera. The prong was set at approximately 1 meter from the extra back-lighting which was used in order to accentuate the edge of the fruit silhouette. The video camera and software were initiated and a series of measurements (taking some 5-10 seconds) were recorded by the program and stored in an ASCII text format file; the whole operation takes around to 2-3 minutes to complete per fruit.

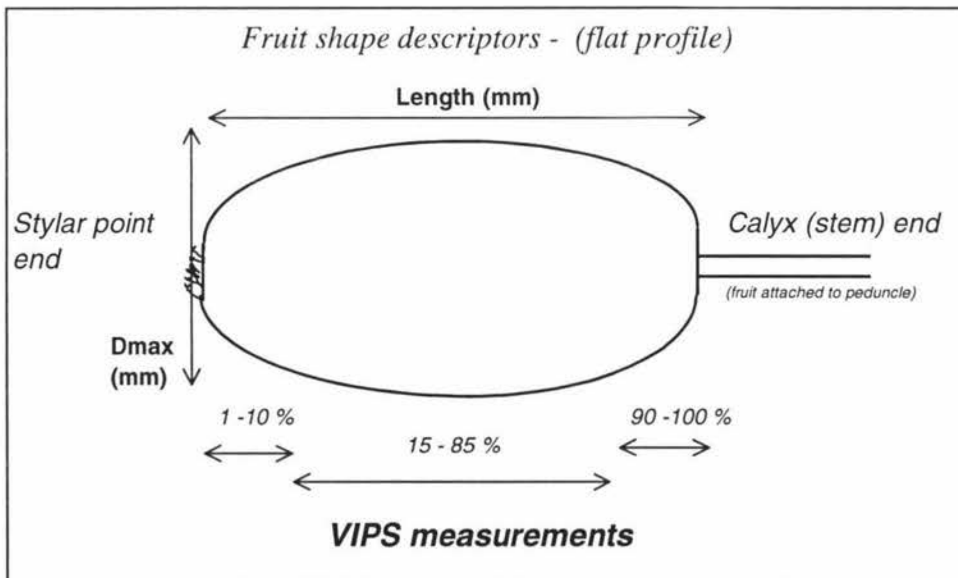
* measurements by the VIP camera are on a percentile basis as follows

Axis length percentile	Percentile intervals	Number of measurements	Cumulative axis
1 -10% 'north pole'	1%	10	1 -10
10 -85%	5%	15	15 -85
90 -99% 'south pole'	1%	10	90 -99

The VIP process also records the length (mm) of the fruit and identifies the widest diameter (dmaxvip). The dmaxvip is different from the DMAXM in the manual caliper measurement, because the former records the percentile at which the widest diameter occurs; but the latter method records the width at 50% (approx.) of the fruits length.

The fruit are placed with the calyx end pointing downward i.e. 'south pole', and therefore, a ratio comparison of the 'north pole' and 'south pole' percentile measurements (1-10% vs 90-99%) determines the degree of difference between these two distal ends. The ratio describes how pointed the 'north pole' is in comparison to the 'south pole'. For example, if the stylar ('north pole') is more pointed than the calyx end then the sum of its' ratio values would be less than 1. Conversely, if the value of the summed ratios were greater than 1, this would indicate that calyx ('south pole') was more pointed than the stylar end.

The "**degree of point**" is classed as end to end comparisons (EENDS). It should be noted, the value EENDS = 1, could be possible when both distal ends are equally pointed. Therefore, it is not strictly a measure of the amount of "point" a particular end has. Another two statistics available from the 35 measurements are the average ratio of the 15,20,25 and 30 percentiles compared to the 75,80,85 and 90 percentiles, this is called the emiddle1 variable (EMID1). The second statistic is the average ratio of the 35,40,45 and 50 percentiles compared to the 55,60,65 and 70 percentiles or emiddle2 (EMID2). Effectively these are the same type of comparison as described for the eends variable, except they concentrate on the comparisons for the main body of the fruit. The following figure illustrates the basic concepts involved in shape descriptor methods used in the FMD study.



*attribute code:***[EENDS; EMID1; EMID2]**
scale : all RATIO measurements

Sensory information

Three fruit were stored independently of the storage assessment fruit, these were used to collect soluble solids content and various subjective taste scores. The fruit were removed from storage and warmed to 18 - 20° C and high humidity (80 - 90%). Once the fruit were assessed as being ready to eat the middle portion of each fruit was tasted and scored for texture (1-5) TEXT and flavour (1-5) FLAV, as listed below. The soluble solids content was measured by taken two drops of juice, from each distal end of the fruit (SENBX). The table below modifies the singular FLAV and TEXT scores into a combined measurement called TAST; or increasing taste acceptability with increasing texture. The TAST variable forms the definition of fruit quality in the current FMD study.

Texture	**1**	**3**	**5**
	grainy floury	O.K.	smooth/melting juicy?
Flavour	**1**	**3**	**5**
	Awful sour/bitter	O.K. mild	Excellent good sweet/acid balance

This 5 x 5 scoring system can be converted to a 1-25 linear scale by the following approach.

				Taste		
	Texture	**1**	**2**	**3**	**4**	**5**
Flavour	**1**	1	2	3	4	5
	2	6	7	8	9	10
	3	11	12	13	14	15
	4	16	17	18	19	20
	5	21	22	23	24	25

attribute code:[**TEXT; FLAV; TAST; SENBX]**
scale : ordinal, ordinal, ordinal (combined) and %SSC

Storage after eight weeks

Following the harvest of each vine, a random sub-sample of twenty fruit was placed in cool-storage. Firmness assessments were taken from three randomly selected fruit of each seedling after eight weeks of storage. The fruit firmness was measured using a 'drill-press mounted' Bryce® penetrometer with an 8mm prod head which measures fruit firmness in kg-force per cm2. Two firmness readings were taken from around the equatorial centre of the fruit , at depth of 2-5 mm's. But firstly the fruit skin was removed (10 mm^2) in slices, one from the fruit at the wide profile and the other from the narrow profile,. The average of these two firmness readings (kg/cm^2) was used to estimate fruit firmness after eight weeks of storage. In addition, the sensitivity of the Bryce® penetrometer could only measure fruit with 0.5 kg/cm^2 force or higher and therefore very soft fruit could not be measured with this instrument. In these cases the soft fruit were equated to 0.5 kg/cm^2, instead of zero, because there was still some response on the penetrometer dial and the zero point was considered inappropriate.

attribute code:[**STR8]]**
scale : ordinal, ordinal, ordinal (combined) and %SSC

Fruit maturity index

In this study, the sequential screening dates were used to ensure that a significantly higher "on-vine" physiological maturity was achieved prior to harvest. The 6.2 %SSC maturity index for 'Hayward' was developed as a minimum rather than an optimum level for a fruit harvest index (Beever and Hopkirk,1990). In fact, it was recommended that a higher level of 7 to 10 %SSC at harvest be used for optimum storage and sensory attributes (Beever and Hopkirk,1990). In this FMD study, the estimate for the time to reach 6.2 %SSC for each seedling is termed its '*maturity days*' and can be estimated from the screening data, provided a number of the following assumptions hold. The procedure for estimating the "time in days to reach 6.2 %SSC", from the datum point of November 1 1995, for each seedling calculated separately, is as follows

1. Plotting the %SSC from the consecutive screening dates, for each seedling separately indicates the rate of change of brix level for the 1996 harvest season. Although there are only 3 points in the graph it is been well documented that the increase in soluble solids concentration follows a non-linear increase as the fruit matures (Beever and Hopkirk,1990).

2. log transformation of the %SSC transforms the non-linear curve into a linear relationship of %SSC and time (in days); the slope (β) was then estimated as the '*slope of the maturity days*' (β_{MD})

3. β_{MD} can be utilised in three different situations (depending on the number of screen dates collected) in order to estimate the time at which each seedling reached 6.2 %SSC; the following equations were used under these three different scenarios

Scenario One

If the screening data has either EBX or MBX < 6.2 %SSC and its LBX is > 6.2 %SSC; then the time at which 6.2 %SSC is reached can be estimated within the range by using the following equation. Where Log(x) is the EBX or MBX %SSC value, and β_{MD} is the slope of its maturity days; **plus** the julian days of the MBX or LBX date in days ("X" is the number of days from the datum point Nov.1 1995).

$$\textit{Maturity days to reach } 6.2\%\text{SSC} = \left[\frac{Log(6.2) - Log(x)}{\beta_{MD}}\right] + \text{days of X}$$

Equation III-1 :Maturity days to 6.2%SSC; where 6.2%SSC falls within range of %SSC monitored over EBX to LBX.

Scenario Two

If the screening data has either its MBX or LBX > 6.2 %SSC; then the time at which 6.2 %SSC is reached can be estimated within the range by using the following equation. Where Log(x) is the MBX or LBX %SSC value and β_{MD} is the slope of its maturity days; **less** the days of the MBX or LBX date ("X" is the number of days from the datum point Nov.1 1995).

$$\textit{Maturity days to reach } 6.2\%\text{SSC} = \left[\frac{(Log(x) - Log(6.2))}{\beta_{MD}}\right] - \text{days of X}$$

Equation III-2 : Maturity days to 6.2%SSC; where 6.2%SSC falls below the range of %SSC monitored over MBX to LBX.

Scenario Three

If the screening data has EBX > 6.2 %SSC or only a single value for its screening data was recorded (i.e. EBX); then the time at which 6.2 %SSC is reached can be estimated within the range by using the following method. Although, there is an assumption that all vines were approximately 4.5 %SSC on the 25 March 1996. This was considered reasonable given those values reported by Pringle *et al.*, 1991 on *A.deliciosa* populations grown at the same site. Therefore the equation becomes a modification of Equation III-1; where 4.5 %SSC is the 'X' value and β_{MD} is the slope of its maturity days; **plus** the days of the EBX date. Furthermore, there were very few cases where the *single* reading (EBX) was less than 6.2 %SSC and in these cases their data was discarded from the analysis.

The maturity days concept comes from the flowering datum day one (November 1 1995) of the previous year up to and including the time to reach 6.2 %SSC (T6_2), for both brix %SSC and dry matter. Consequently, the 1996 estimated day value, for HVBX or T6_2, has 61 days added to it and this gives the maturity days from the datum flowering point. This arbitrary bench-mark was chosen to keep it consistent with the time data used for flowering. In this FMD study then, the "maturity days" refers to the number of days from November 1, 1995 up to its estimated time to 6.2 %SSC (T6_2). In addition the dry matter content at T6_2 can also be estimated from the screening data, in an analogous, fashion to that described above for T6_2. However, the T6_2 is used and interpolated with the dry matter curve to estimate its D6_2. Consequently, a comparative statistic for the day at which each vine reached 6.2 %SSC (T6_2 & D6_2) can be estimated.

attribute code: **[T6_2; D6_2]**
scale : No. of days and %DM

Vines with less than 10 fruit

There were over 300 vines with less than 10 fruit from the 916 female vines in 1996 and these were not 'screen tested' but were instead harvested in the first week of May 1996. Total yield, mean fruit weight and shape descriptors were collected on fruit from these vines. In addition, if sufficient fruit were available, post harvest assessments of sensory and storage was also done, however, data from these vines was not included in the analyses.

D. ANOVA of vegetative and fruiting characters

The univariate analyses of the ten selected vegetative and seventeen fruiting characters were used to estimate GCA/SCA effects, maternal effects, heritabilities and their standard errors. These data were analysed using the GLM procedure in SAS® (SAS Inst., Cary, N.C. 1989) to partition the relevant sums of squares for their respective reduced FMD designs and as based on the a single season environment model (Equation III-3). The cross-classified nature of the experiment allows two estimates of the additive genetic variance. The first is the *female* classifier i.e. by female parent, and the second on is the male classifier i.e. by male parent, for their respective main effects. Furthermore, pooling these sum of squares and their relevant degrees of freedom can be used to calculate a combined *female/male* narrow sense heritability (Hallauer and Miranda, 1981). These variance components can be used to determine the presence of maternal effects. Hallauer and Miranda (1981) proposed that the maternal effect may be estimated by dividing the *females* (GCA) component by the *males* (GCA) component, although, the presence of maternal effects are not necessarily due to classical maternal effects alone.

Falconer, (1989) describes the classical maternal effects variation as external effects due to a 'common environment', such as nutritional aspects of mothers and their offspring in mammals. In this case, the covariance of the mother's phenotypic value for a character can effect the value of the same phenotypic character in the offspring. Wricke and Weber (1986) also suggested that these transient maternal effects might instead reflect differences in inbreeding levels of the various parents. Clearly, several different hypotheses exist which attempt to explain the variation caused by these maternal effects. The maternal effects test for these characters were estimated and are included in the partitioned variance component tables in Chapter 4. The model statement and expected mean squares table below (Table III-5 and Equation III-3) relates to the FMD crossed classified experimental design in a single environment, for a random inference base model (from Hallauer and Miranda 1981). The FMD design is considered a infinite random effects model, as the parents were chosen at random from a diverse range of the *A. deliciosa* gene pool in New Zealand.

Several assumptions were made, about the reference population being studied, in order to interpret the genetic variance components from the relevant variance components as follows

- regular diploid behaviour at meiosis
- no multiple allelism
- linkage equilibrium, i.e. no correlation of genotypes at separate loci
- no epistasis i.e. effect of variation in genotype at any single locus is not modified by genes at other loci (from Comstock and Robinson, 1948).

Table III-5 : Expected mean squares for a randomised complete block, factorial mating design in a single environment [infinite random] (from Hallauer and Miranda, 1981).

Source of variation	d.f	Expected mean squares	M.S	v-ratio
blocks	r-1	$(\sigma^2_w + n\sigma^2_e) + nfm\sigma^2_r$	5	5/1
female (parent)	f-1	$(\sigma^2_w + n\sigma^2_e) + nr\sigma^2_{f.m} + nmr\sigma^2_f$	4	4/2
male (parent)	m-1	$(\sigma^2_w + n\sigma^2_e) + nr\sigma^2_{f.m} + nrf\sigma^2_m$	3	3/2
female x male	(f-1)(m-1)	$(\sigma^2_w + n\sigma^2_e) + nr\sigma^2_{f.m}$	2	2/1
error (a)	(r-1)(fm-1)	$(\sigma^2_w + n\sigma^2_e)$	1	-

σ^2_e = between plot error variance σ^2_w = within plot genetical variance + within plot environmental variance: $\sigma^2_w = \sigma^2_{wg} + \sigma^2_{we}$; where $\sigma^2_{wg} = \sigma^2_G$ - *Cov* (FS) ; and σ^2_{we} is the environmental variance; σ^2_{we} is estimated using the method described by Testolin *et al*., (1995).

Many of these parents were selected directly from the 'wild' *A. deliciosa* populations of China, and are assumed to be close to '*panmictic*' expectations. Subsequently, these parents are likely to be highly heterozygous for various traits and are expected to be in linkage equilibrium (Ferguson *et al.,* 1996;; Hallauer and Miranda, 1981). The failure of certain assumptions is inevitable, however, understanding the implications of these failures and how they might effect the genetic analyses is crucial.

For example, the failure of linkage equilibrium has the effect of an upward bias in the estimation of the dominance variance (Comstock and Robinson, 1952). This is especially so if the linkage groups are in the repulsion phase (Dudley and Moll, 1969). Falconer (1989) indicates the closer the linkage, the greater the increase in the interaction or dominance component. The model below is typical of a RCB two factor factorial with two separate error terms. The whole plot or residual error (a) is the most important error term for any variance F-tests that are performed in the FMD data analyses (Table III-5).

Model

$$Y_{ijkl} = \mu + \rho_k + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ijk} + \varpi_{ijkl}$$

Y_{ijkl} = phenotypic observation, of the ith female and the jth male in the kth replicate on the lth seedling.
μ = overall mean effect for Y
ρ_k = k[th] block (replicate) effect
α_i = i[th] female parental effect (*main factor A*)
β_j = j[th] male parental effect (*main factor B*)
$\alpha\beta_{ij}$ = i[th] female x j[th] male parental combination (*1st order interaction effect*)
ε_{ijk} = error (a) residual effect (*whole-plot error*)
ω_{ijk} = sub-samples (within plot) internal segregates, i.e. Full sib plants

Equation III-3 : Model Statement for FMD single environment experiments (from Hallauer & Miranda, 1981).

The additive genetic variance σ_A^2 at a single locus is the variance caused by the weighted linear regression of genotypic values on a number of favourable alleles and the dominance variance being considered deviations from the regression. In addition, if the total genetic variation over many loci is larger than the sum of the individual loci (for additive and non-additive effects), then the difference will be the variance due to epistasis. The epistatic effects can also cause an upward or even downward bias in the estimation of the dominance component. However, the magnitude of the bias has been considered small in comparison to the actual genetic variation (Comstock and Robinson, 1952).

1. Significance testing of variance components

The sums of squares are partitioned into their respective sources of variation, as determined by the model statement (Equation III-3 and Table III-5). The significance of the *F-test* is calculated by the 'user defined' GLM procedures *test* option in SAS®, which in effect overrides the SAS® default tests that always use the last error term.

The *F-test* probabilities are found directly by the *test* option, in the GLM procedures of SAS ®. These *F-test* probabilities are calculated by using a synthetic *F-test* whereby the denominator is a linear function of mean squares (including negative variance components) and a synthetic Satterthwaite degree of freedom is calculated for this linear function (Littell *et al.,* 1991).

2. Expectations of mean squares for vegetative characters

The internal replication imbalance meant some vegetative characters had less than 6 plants per plot being measured and used to estimate the plot mean. As a result, the mean (harmonic) plant numbers per plot varied from 3.89 to 5.91 in Factorial One and 4.11 to 5.87 in Factorial Two. The vigour associated measurements such as trunk diameter (MM93-MM96) and prominent bud counts (PRBD) were obtained from almost every plant (~6 plants per plot). However, the floral attributes were measured from a lesser number of plants (~4 plants per plot), because on average 68% of the total plants were sexually mature across both factorials. Clearly the fruiting data (being based on the females) has an even lower number of ~2 plants measured per plot. In order to calculate the variance component of interest, both the *random* statement and *test* option are used in the GLM analysis. The former provides an estimate of the respective coefficients and these are then pre-multiplied to each variance component of the linear independent mean squares equations. The *test* option overrides the SAS® default *F-test* error term and allows a 'user defined' error term to be specified. These are presented in the v-ratio column of Table III-5. These estimated variance components can then be used to determine the additive genetic variance, as a proportion of the total phenotypic variance, V_a/V_p, narrow sense heritability or simply heritability by using the relatives covariance approach (Becker 1992; Falconer 1989)

Harmonic weighting adjusts the numerator of the *F-test* with respect to the denominator of the test (Gordon, *pers. comm.*). This is especially useful when the internal replication imbalance is more severe. Consequently, each variable has its own weighting of harmonic means, and therefore, slightly different coefficients as follows. In addition, the AGR and CU96 variables, which are mathematical manipulations of the vigour measurements, have very similar harmonic weightings; therefore the CU96 shall be presented here as being equal to those coefficients for AGR.

The use of the reduced FMD analyses has ensured that the imbalance has been minimal in the vegetative characters. This is evidenced by the weighting factors being close to unity. However this is not the case in the fruiting data (see Chapter 3), as the inherent problems of imbalance are further complicated by the low number of female vines mature in 1995 flowering and also their distribution amongst the plots. The pooling of the main effects in the vegetative data analyses is possible because there are equal degrees of freedom in both the male and female effects of the reduced FMD designs. This is illustrated by the coefficients for both the male and female effects being very similar save rounding errors.

3. Example of variance component estimation

The preceding sections described the methods involved in partitioning the variance components for each expectation of mean squares. This section illustrates the method used in deriving the variance component estimation for the variable PRBD (prominent bud count), from the reduced Factorial One 5x5 analysis; using these mean squares and their harmonic mean (weighted) information. The calculations involved in estimating the standard error of these respective variance components is also given.

Example of PRBD variable in F1 v 5x5 FMD analysis

Variance due to Block (REP) effect

$$V_{[REP]} = \frac{1}{\text{Coeff.}} \times [\,\mathbf{MS}_{\mathbf{REP}} - \mathbf{MS}_{\mathbf{Resid}}\,]$$

Coefficient$_{\mathbf{Rep}}$ = **(f x m x n)** from E(MS) harmonic means in RANDOM statement SAS®. also mean squares used here are adjusted for by their harmonic average

$$V_{[REP]} = \frac{1}{142.9151} \quad [57.1501 - 4.881]$$

$$= 0.0069 \quad [52.2691]$$

$$= 0.3657$$

$$\text{S.E} = V_{\{V_{[REP]}\}^{1/2}} = \sqrt{\frac{2}{(142.9151)^2}\left[\frac{(57.1501)^2}{5+2} + \frac{(4.881)^2}{120+2}\right]}$$

$$= \sqrt{0.0001\ [466.786\ ]}$$

$$= \sqrt{0.04571}$$

$$= 0.2138$$

$$\text{i.e. } V_{[REP]} = 0.3657 \pm 0.2161$$

Variation due to Female (MHS) effect

$$V_{[MHS]} = \frac{1}{171.7602} \quad [16.5256 - 7.0672]$$

$$= 0.00582 \quad [9.4584]$$

$$= 0.0551$$

$$\text{S.E} = V_{\{V_{[MHS]}\}^{1/2}} = \sqrt{\frac{2}{(171.7602)^2}\left[\frac{(16.5256)^2}{4+2} + \frac{(7.0672)^2}{20+2}\right]}$$

$$= \sqrt{0.00007\ \ [47.7861]}$$

$$= \sqrt{0.00324}$$

$$= 0.0569$$

$$\text{i.e. } V_{[MHS]} = 0.0551 \pm 0.0569$$

Variation due to Male (PHS) effect

$$V_{[PHS]} = \frac{1}{171.7456} [24.9179 - 7.0672]$$
$$= 0.00582 \quad 17.8507$$
$$= 0.1039$$
$$\text{S.E} = V_{\{V_{[PHS]}\}^{1/2}} = \sqrt{\frac{2}{(171.7456)^2}\left[\frac{(24.9179)^2}{4+2} + \frac{(7.0672)^2}{20+2}\right]}$$
$$= \sqrt{0.00007 \; [105.751]}$$
$$= \sqrt{0.00717}$$
$$= 0.0847$$

i.e. $V_{[PHS]} = 0.1039 \pm 0.0847$

Variance due to Female x Male (MHS*PHS) effect

$$V_{[MHS*PHS]} = \frac{1}{34.3180} [7.0672 - 4.881]$$
$$= 0.02914 \quad 2.1862$$
$$= 0.0637$$
$$\text{S.E} = V_{\{V_{[RMHS*PHS]}\}^{1/2}} = \sqrt{\frac{2}{(34.3180)^2}\left[\frac{(7.0672)^2}{20+2} + \frac{(4.881)^2}{120+2}\right]}$$
$$= \sqrt{0.0017 \; [2.4661]}$$
$$= \sqrt{0.004187}$$
$$= 0.647$$

i.e. $V_{[MHS*PHS]} = 0.0637 \pm 0.0647$

Variance due to Error(a) (whole plot) effect

$$V_{[error(a)]} = \frac{1}{5.7413} [4.881 - 4.3083]$$
$$= 0.1742 \quad [0.5730]$$
$$= 0.0998$$
$$\text{S.E} = V_{\{V_{[error(a)]}\}^{1/2}} = \sqrt{\frac{2}{(5.7413)^2}\left[\frac{(4.881)^2}{120+2} + \frac{(4.3083)^2}{713+2}\right]}$$
$$= \sqrt{0.0607[0.2212]}$$
$$= \sqrt{0.0134}$$
$$= 0.1159$$

i.e. $V_{[error(a)]} = 0.0998 \pm 0.1159$

As explained earlier, the harmonic weighting factors were pre-multiplied across the respective linear mean squares and their coefficients. These *adjusted* values were used in the estimation procedures described above. The reasons for this adjustment have been discussed in Section B, on problems of imbalance in the vegetative and fruiting data sets. Therefore the reduced FMD designs have approximated this "balanced" analysis, given the constraints of the data. The variance component estimates were used for all the vegetative and fruiting data collected during the 1995-1996 FMD study. Accordingly, these results are presented in Chapter 4, without further explanation.

4. Estimating the within plot genetic variance

Testolin *et al.,* (1995) estimated the genetic fraction (*gkg*) of the within plot variance as 0.5 $V_{additive}$ + 0.75 $V_{dom.}$ after using a similar 'single season environment' factorial design. The estimate of the genetic fraction (*gkg*) is possible because the total genetic variation less the variation due to the covariance of full sib (COV_{FS}) leaves 0.5 $V_{additive}$ + 0.75 $V_{dom.}$ as well as 0.75 $V_{add.\ x\ add}$ plus other epistatic components (if present) Hallauer and Miranda (1981).

Characters that had very high additive genetic variation such as MEDF, also had very high genetic fraction *gkg* estimates. In these instances, there was a significant interaction effect recorded and this could have inflated the additive variance estimate, because the additive variance estimate contains some of the epistatic variance (~0.25) as well. Consequently, this method of estimating the genetic fractions *gkg*, can actually lead to larger variance estimates than the *within plot* variance, in some cases. Clearly, this was not appropriate and therefore a reduction of the formula was used instead i.e. 50 or 25 % reductions wherever necessary.

The best within-plot genetic fraction can be estimated from a concurrent replicated parent-offspring (POR) trial (not conducted during this study). This not only estimates the genetic fraction in the plots but also allows the estimation of the upper limits of heritability.

The factorial mating design is not able to partition these non-additive variance epistatic effects from the dominance effects as such. Therefore, its not surprising that the estimate of *gkg* overestimates this component, particularly when there is a significant first order interaction effect reported. In addition, this also helps explain how a narrow sense heritability estimate in excess of 1 can be reported, in the FMD study.

E. Genetical estimates of characters

1. Heritability estimates

The narrow sense heritabilities for the vegetative and fruiting characters can be estimated from the method outlined in the preceding sections D.2 to D.4. If data is collected on an individual plant basis (as it is in the FMD study), then these plants form the basic "selection unit" from which the heritability is estimated. Hallauer and Miranda (1981) describe this as the individual plant heritability estimate. The formula for estimating the heritability on an individual plant basis in a factorial mating design is given by

$$h^2_{ind.f(m)} = \frac{4\sigma^2_{f(m)}}{\sigma^2_w + \sigma^2 + \sigma^2_{fm} + \sigma^2_f + \sigma^2_m}$$

Equation III-4 : Heritability based on an individual plant basis (Hallauer & Miranda, 1981)

The best estimate of heritability is obtained from the pooling of male and female sums of squares and their respective degrees of freedom. The approximate standard error of a variance ratio given by Dickerson's method in Hallauer and Miranda (1981), is usually a conservative estimate (see Equation II-14). In addition, small negative or positive variance component estimates are sometimes equated to zero in the literature (Gordon *et al.*, 1972; Searle, 1971). Reporting of these non-truncated estimates can be unsatisfactory, although, in some cases unavoidable. Searle (1971) describes the problem of negative estimates, is that they can lead to a bias in the final estimate. Furthermore, Searle (1971) postulated that different statistical techniques could also be employed, such as Bayes estimators or the maximum likelihood analyses, to alleviate the problem. The reporting of negative variance component estimates have been less of a problem in the vegetative data than compared to the fruiting data. This is due in part to the higher level of imbalance in the fruiting data as compared to the vegetative data.

2. GCA mean and variance based estimates

General combining abilities of means (GCA_{mean}) were calculated using the following methods for each character separately amongst the two reference populations, these various statistics give an indication of the breeding value of the respective parents. The plant breeder may be interested in improving a certain character, by either increasing or decreasing its numeric value. Therefore, some method for discriminating between these BiP means is necessary, if the best half sib family is to be selected. Accordingly, the least squares means (LSM's) statement and PDIFF option (or probability of a difference) in the GLM procedure of SAS® was used to test the null hypotheses of no difference Ho : $LSMi = LSMj$ between two means i and j.

These LSM's and PDIFF probabilities can be used to test the significance of each source of variation. Therefore testing for any significant differences between each source of variation of male, female and interaction terms is possible. The comparisons of male and female arrays, in effect, are testing for differences (or similarities) between the GCA_{mean} breeding values **amongst** these parents. Alternatively, comparisons of male by female interactions, in effect, are testing for differences (or similarities) between the SCA_{mean} breeding values **within** these parental arrays.

a) Significance testing of GCA (means)

The GCA_{mean} effects for family comparisons must first a have statement made as to the probability level (PDIFF) at which these means should be "considered" significantly different. I have chosen a 10% significance level (or less) as the point at which a biological effect can be considered 'real'. The PDIFF $Pr \leq 0.10$ has been chosen for GCA_{mean} (LSM) as describing that a significant difference exists **between** two half sib family arrays. In addition, if two half sib parental arrays are different from each other, as well as from all other half sibs, then several significant GCA effects can co-exist. However, if the two half sib arrays are different from the rest of the parental arrays but not different from each other (i.e. they are 'alike'), I have nominated that their 'likeness' must be significant by a probability of $Pr \geq 0.90$.

Therefore, two separate half sib arrays can be considered to have a similar breeding value if their parental arrays have a significant difference (PDIFF) of $Pr \geq 0.90$ i.e. they are the same at the 90 % significance level. Using this method of means discrimination the GCA_{mean} trends can be ratified by both their ANOVA significance tests and their least squares means probabilities of a difference (PDIFF) results. This is a similar technique to that of the '*Fishers protected test*' procedure outlined by Steel and Torrie (1980).

b) Significance testing of SCA (means)

The following procedure was used to ascertain if a particular BiP was performing outside of the general combining ability of the line (parental array) i.e. testing for a significant specific combining ability effect (SCA_{mean}). Subsequently, each and every BiP mean must be compared to test their PDIFF values. For example, F1 v 5x5 reduced design has 25 separate BiP means, and PDIFF values for 300 combinations are tested for each variable. This method allows us to test if a SCA_{mean} effect is significant **within** a half sib arrays.

The 10% significance level (or less) was again used to test for the SCA_{mean} effect. In comparing a certain BiP as being significantly different at the 10% level, against **ALL** other half sib family means, then a similar procedure to the GCA_{mean} method above was used; and was as follows

- comparing (*n* families) the PDIFF $Pr \leq 10\%$ of the BiP in question across ALL its' half sib relatives; if it is significantly larger (or smaller) than the remaining families it can be considered as having hybrid vigour and performing outside of the GCA family performance
- testing the remaining families (*n*-1) amongst themselves at the PDIFF of $Pr \leq 10\%$, any BiP considered to have a PDIFF $Pr \leq 10\%$; it could have an opposite SCA effect to the **first** SCA effect or alternatively it must **also** have a PDIFF of $Pr \geq 0.95$ in comparison with the **first** SCA family identified i.e. it must be of the direction as the **first** SCA effect, this gives a measure of 'likeness' between two SCA families

Significant differences between individual combinations of families (BiP's) *within* a GCA line can still exist although it may not necessarily indicate that there is a significant SCA effect, is unless the above criteria are satisfied.

c) *Significance testing of GCA/SCA (variance)*

The GCA_{var} main effects (additive genetic) and the SCA_{var} (non-additive genetic) variance, both have their *F-test* significance tabulated by testing their respective expectation of the means (EMS) by the appropriate ratio of for the test statistic (as outlined in Table-II-2). This *F-test* significance is set at the 5% and 1% significance levels. In addition the actual estimates of the respective components by female, male and interaction (fem.x male) are also estimated and tested for their significant difference from zero. The ratio of the GCA_{var} / SCA_{var} can be used to indicate the relative differences between these sources of variation and their relative importance in determining the genetic properties of a population for a particular character.

In addition, the usefulness of these significance tests can be seen when applying their findings together with the GCA_{mean} type information. For example, if a certain character shows a highly significant non-additive or SCA_{var} effect, then the respective BiP's being identified by the SCA_{mean} results, for hybrid vigour tests are expected to be very "real". This approach is similar to the '*Fishers protected F-test*' and shows how both the mean and variance GCA/SCA results can be used together in order to determine the genetic properties of the populations. Consequently, equal emphasis is placed on the results of both the GCA/SCA effects from their means and variance based information. Although the derivations for GCA/SCA effects from means and variance based information, are very different it still is possible to utilise both sets of results in order to understand the general worth of these respective parents in the FMD study. Because if a significant GCA/SCA_{var} effect is present, then it is important to know where these effects are actually being expressed, therefore, the GCA/SCA_{mean} effects are equally important.

F. Summary

The vegetative data was mostly collected from the 1995 flowering season and the fruiting data were collected from the 1996 fruit season. The methodology for collection of these data has been given in the preceding section. The data were analysed using the GLM procedure in SAS® and genetical interpretation was done by those methods outlined in Hallauer and Miranda 1981. In general, the vegetative data was much more suited to the analyses compared to the fruiting data. There were a number of issues that affected the imbalance problems of the fruiting data these included

- insufficient number of seedlings planted out in certain BiP's
- dioecious nature of the species and the random distribution of female vines per plot
- low sexual maturity of the population and the tendency for a male bias in the sex ratio
- insufficient crop loads for the complete suite of characters to be tested on all vines

These issues compromised the data sets and the reduced design analyses were employed. However, the analyses of the single 1996 fruit data season will still provide several statistics for genetical interpretation. In addition, as the number of sexually mature plants increase and subsequently the number of female vines measured are also expected to increase then a more reliable set of statistics can be estimated and confirm any early findings from this FMD study.

IV. Results and Discussion

The following Chapter will present the results from the 1996 fruit data season for vegetative and fruiting data separately. The unbalanced data sets for the vegetative and fruiting data has meant reduced FMD designs were employed. However, this imbalance was less noticeable in the vegetative data as compared to the fruiting data. These issues were covered in Chapter 3- *Materials and Methods*. In addition, the data has firstly been analysed on a population basis in order to establish their differences and to clarify the reason for treating the two sub-populations separately. Consequently, these analyses will then be divided into two main areas; vegetative and fruiting characteristics and the results presented as follows.

A. Vegetative data results

Table IV-1 summaries the descriptive population statistics for ten vegetative characters in Factorial One (reduced FMD) of F1 v 5x5 and Factorial Two (reduced FMD) of F1 v 6x6. These data are the unadjusted population means for the two reduced FMD sets. The 5x5 reduced FMD for Factorial One included maternal parents A, B, C, H and M and paternal parents 01, 06, 07, 09 and 13. The 6x6 reduced FMD for Factorial Two included maternal parents F, I, J, K M and N and paternal parents 03, 04, 05, 08, 11 and 14 (Appendix A: Tables V-3 and V-4).

The populations mean comparisons show that all variables are different between the two reference base populations (IBP's). Their means are different as judged by the confidence limit between each pair of means, at the 0.1 % significance level (*for a two-tailed test*). From these %C.I $t_{0.001}$ it can be seen that all vegetative characters measured in both reference populations have significant differences between them. Therefore it would be wise to analyse these IBP's separately in order to estimate their respective genetic statistics. These phenotypic differences can be due to their genetic and environmental backgrounds. Considering the data is collected over the same site and at the same time, it is unlikely that the environment is a major reason for the difference. There is an assumption that the macroenvironment is relatively uniform.

Table IV-1 : Population statistics for ten vegetative characters in Factorial One 5x5 and Factorial Two 6x6 designs.

Factorial One [5x5]

Variable	mean	unit	±2SE	std dev.	n	min	max
PRBD	8.003	0.001	0.151	2.214	863	2.5	16.5
JVPD	2.554	0.001	0.042	0.504	589	1.0	3.0
MEDF	15.013	0.001	0.344	4.194	595	6.15	30.0
FRNG	9.498	0.001	0.406	4.956	595	2.0	25.0
CU96	24.189	0.001	0.388	5.735	875	6.3	48.3
AGR	2.774	0.001	0.013	0.188	878	1.9	3.3
MM96	31.411	0.001	0.402	5.979	887	12.7	55.3
MM95	22.496	0.001	0.331	4.935	887	8.8	40.0
MM94	13.525	0.001	0.180	2.675	888	6.4	25.4
MM93	7.229	0.001	0.086	1.282	884	3.1	12.2

Factorial Two [6x6]

Variable	mean	unit	±2SE	std dev.	n	min	max
PRBD	6.997	0.001	0.119	2.082	1219	1.5	16.5
JVPD	2.276	0.001	0.036	0.542	926	1.0	3.0
MEDF	23.891	0.001	0.317	4.774	905	9.0	38.3
FRNG	11.615	0.001	0.350	5.270	905	2.0	28.0
CU96	25.576	0.001	0.355	6.245	1235	7.3	45.2
AGR	2.810	0.001	0.011	0.194	1242	2.0	3.3
MM96	30.010	0.001	0.398	7.079	1266	13.1	56.4
MM95	24.478	0.001	0.350	6.226	1266	8.1	43.3
MM94	14.781	0.001	0.223	3.965	1270	3.0	30.0
MM93	7.505	0.001	0.103	1.824	1262	2.5	13.0

Table IV-1 illustrates the number of vines measured in each case (**n**) and the fact that both populations have similar ranges (**max. – min.**) and standard deviations (**std dev.**) for the ten vegetative characters. However, in comparing the first degree statistics (**means**) between the various characters in both populations, it is evident that there are significant differences between the two data sets as judged by their t-test (**unit**) probabilities. These differences are not the main focus in the current FMD study, however, this result confirms the need to analyse these data separately.

Table IV-2 : Trends in the differences between the means of ten vegetative characters across Factorial One (5x5) and Factorial Two (6x6).

Level of difference	**Variable**	**Factorial One Means (5x5)**	**Factorial Two Means (6x6)**
Large	MEDF	15 Nov 1995	24 Nov 1995
	FRNG	9.5 days	11.6 days
Moderate	PRBD	8 buds per 500 mm	6 buds per 500 mm
	JVPD	2.6 years to flowering	2.3 years to flowering
Small	CU96	*similar	*similar
	MMYR's		

**Trunk diameters (MMYR's) followed the same trend, but Factorial Two (6x6) has a slight advantage in cumulative trunk diameter (size), CU96.*

Comparisons made on a population basis reveal that Factorial One has an earlier flowering date, shorter flowering range, more buds per 500 mm cane and is less precocious compared to Factorial Two. The differences in cumulative trunk diameters are less obvious, although overall, Factorial Two appears to have slightly larger cumulative trunk diameters, conversely, the final trunk diameters (MM96) has Factorial One with a slight advantage.

These results show the differences amongst the respective gene pools from which these parents originate. Factorial One is less diverse in its origins (geographically), than compared to Factorial Two and is further complicated by some possible relatedness in the pedigree lines of various parents. Therefore the degree of coancestry in Factorial One is slightly higher compared to Factorial Two, although this is not expected to invalidate the genetical assumptions given earlier. In addition, the seed extraction, seed raising and planting procedures may also have unwittingly grouped the families into early (*Factorial One*) and late (*Factorial Two*) sets. The earlier maturing BiP's were extracted sooner and therefore had a longer growing season in the fast-track system (see Chapter One) compared to the later maturing BiP's. It is possible that these effects could be carried over into the population performances and for these reasons the dual analyses has proceeded.

1. Sexual maturity and sex ratios

The following Table IV-3 is a summary of the sexes based on half sibs (factor A or female parent). From the 1995 flowering season all individual plants were strictly classified as either male, female or immature. The maternal half sib family maturities for Factorial One vary from 38% to 87%, with a female to male ratio of 1:1.30 and an overall maturity of 63%. Similarly in Factorial Two, maternal half sib family maturities varied from 48% to 84%, with a female to male ratio of 1:1.34 and an overall maturity of 73%. Each maternal half sib family line was chi-tested χ^2 for the probability of the female to male ratio being equal to 1:1 i.e. H_o = *1:1 Female:Male*. Almost half of the family lines' chi-square tests were significant, Pr ($\chi^2 \leq 0.05$), thus rejecting the null hypothesis of an expected female to male ratio of 1:1. However it should be noted that the overall maturity is 68% and that given this level of sexual maturity it is not surprising that the null hypothesis of a 1:1 ratio is rejected. Sampling variation during seedling selection at the post-germination stage can lead to either a male or female bias of the final ratios. The average female to male ratio of 1:1.32 was reported *across both* Factorial designs. Consequently, more male vines had flowered than female vines (32% more in fact) in spring 1995. This type of male bias occurs frequently in the early part of the generation cycle of seedling populations of *Actinidia* (Ferguson *et al.*, 1996). In contrast Beatson (1991) reports up to 1:1.5 ratio as being typical of *A.deliciosa.* Although, in my experience, while sampling variation can sometimes produce high individual family ratios (i.e. 1:1.5), the overall population ratio almost always approaches 1:1 (Pringle *et al.*, 1991). Testolin *et al.,* (1995) also reported the final sex ratio does approach 1:1 at full maturity. If this hypothesis is correct, then we would expect that more females are **yet** to flower in the FMD study. Currently, almost 2,100 plants from the 3,100 have flowered in 1995, leaving some 1,000 vines left to flower. Clearly, if the final female to male ratio is to approach the 1:1 ratio as suggested by Testolin *et al.,* (1995), then, 650 females are expected to flower out of the remaining 1000 immature vines. Early indications from the 1996 flowering season suggests that this is very likely, with the 1996 flowering ratio approaching 1:1.1 at 90% maturity (Appendix A: Table V-1). The trend in higher precocity being associated with Factorial Two (73%) as compared to Factorial One (63%) is in agreement with the previous results for the juvenile period, JVPD in Table IV-1. This is further evidence that there are some basic genetical differences between

these two populations. Factorial Two parents appear to have contributed a greater abundance of the *more* alleles for precocity as judged by the differences in their percentage of sexually mature vines and by their shorter juvenile period, on a population basis.

Table IV-3 : Summary of 1995 sex ratios for all maternal arrays in Factorial One and Two.

Summary of 1995 Flowering Season								
Maternal Array								
Factorial One	**Female**	**Male**	**Imm.**[1]	**F:M**[2]	**%Mat**[3]	**Pr(χ^2)**[4]	**NP**[5]	**Total**[6]
A - 40-4-13f	43	82	127	1.91	**0.50**	0.00	3	255
B - Tomua	76	79	66	1.04	**0.70**	0.81	31	252
C - 47-5-10f	92	110	50	1.20	**0.80**	0.21	0	252
D - 3-6-20b	41	72	100	1.76	**0.53**	0.00	36	249
E - 40-1-16a	36	51	143	1.42	**0.38**	0.11	22	252
H - 36-4-0b	65	79	86	1.22	**0.63**	0.24	22	252
M - Bruno	100	117	33	1.17	**0.87**	0.24	2	252
Total	**453**	**590**	**605**	**1.30**	**0.63**	**0.24**	**116**	**1764**
Factorial Two	**Female**	**Male**	**Imm.**	**F:M**	**%MAT**	**Pr(χ^2)**	**NP**	**Total**
F -3-6-11b	75	102	65	1.36	**0.73**	0.04	10	252
I - 3-2-10b	96	87	67	0.91	**0.73**	0.51	2	252
J - 3-2-11a	76	117	57	1.54	**0.77**	0.00	2	252
K - Jumbo	36	71	118	1.97	**0.48**	0.00	27	252
M - Bruno	83	122	39	1.47	**0.84**	0.01	8	252
N - C6M2	89	111	48	1.25	**0.81**	0.12	8	252
Total	**455**	**610**	**394**	**1.34**	**0.73**	**0.00**	**53**	**1512**
Grand Total	***908***	***1200***	***999***	***1.32***	***0.68***	***0.00***	***169***	***3276***

Imm. [1]=immature F:M[2] = female to male ratio %Mat[3] = % mature Pr (χ^2)[4] = probability of ratio 1:1 NP[5]= either not planted or died after planting Total[6] = number of plants in a BiP of a full set

2. GLM - ANOVA of vegetative data

a) Combining abilities GCA_{var} and SCA_{var}

The ANOVA tables for the ten vegetative characters are presented below. The mean squares are partitioned into their respective sources of variation, as determined by the model (Equation II-3) and the estimated mean squares are given as follows (Table IV-4).

Table IV-4 : Estimated mean squares of ten vegetative characters and their F-test significance.

			Factorial One [5x5]			
Variable	σ^2_{blk}	σ^2_{fem}	σ^2_{male}	$\sigma^2_{fem*male}$	$\sigma^2_{error(a)}$	σ^2_{resid}
PRBD	57.42 **!	16.56 (*)	25.02 *	7.10	4.88	4.31
JVPD	0.72 *	0.36	0.78 (*)	0.301	0.26	0.24
MEDF	69.08 **!	447.02 **!	215.80 **	42.41 **!	12.36	11.62
FRNG	96.76 **!	423.55 **!	86.31 *	18.92	20.73	21.32
CU96	151.14 **!	707.76 **!	599.06 **!	37.92 *	20.44	27.16
AGR	0.20 **!	0.77 **!	0.55 **!	0.04 (*)	0.02	0.03
MM96	103.86 **!	735.16 **!	650.97 **!	44.11 *	24.03	29.91
MM95	133.71 **!	448.21 **!	258.62 **!	29.49	20.59	24.35
MM94	25.90 **!	126.27 **!	33.11 *	8.91	7.30 (*)	6.13
MM93	9.34 **	7.61	7.61	3.60	2.40 **!	1.36
			Factorial Two [6x6]			
Variable	σ^2_{blk}	σ^2_{fem}	σ^2_{male}	$\sigma^2_{fem*male}$	$\sigma^2_{error(a)}$	σ^2_{resid}
PRBD	78.23 **!	10.92	40.94 **!	6.24 (*)	3.99	3.75
JVPD	1.76 **!	5.97 **!	1.99 *	0.574 *	0.35 **!	0.21
MEDF	120.74 **!	1292.93 **!	471.26 **!	44.61 **!	14.12 *	11.49
FRNG	125.44 **!	76.56	94.98	44.90 *	27.25	25.74
CU96	514.81 **!	929.75 **!	708.52 **!	91.11 **!	36.39 **	28.09
AGR	0.41 **!	0.91 **!	0.65**!	0.09 **!	0.03	0.03
MM96	1060.03 **!	1378.02 **!	775.22 **!	134.86 **!	52.44 **!	32.96
MM95	1502.46 **!	1100.30 **!	325.98 *	112.93 **!	40.14 **!	23.15
MM94	593.96 **!	440.32 **!	154.44 (*)	63.13 **!	21.38 **!	8.16
MM93	107.54 **!	93.60 **	33.47	17.40 **!	5.98 **!	1.50

Key: F-test probabilities for significance
Pr < 0.001 = **!, Pr < 0.01 = **, Pr < 0.05 = * and Pr < 0.10 = (*).

The significance of the *F-test* is calculated by the 'user defined' GLM procedures *test* option in SAS®, which in effect overrides the *SAS® default tests*. The SAS *default test* uses the last error term for all its *F-tests* and this test method is not appropriate to the FMD model. The *F-test* probabilities for these estimated mean squares are found directly by the *test* option in the GLM procedures of SAS ®. These *F-test* probabilities are calculated by using a synthetic *F-test* whereby the denominator is a linear function of mean squares (including negative variance components) and a synthetic Satterthwaite degree of freedom is calculated for this linear function (Littell *et al.,* 1991).

The results from the ANOVA in both reference populations showed that 'blocking' (RCB) was effective in removing variation due to replicates for ALL vegetative variables. The replicate effect was much greater in Factorial Two as compared to Factorial One, especially for the various vigour measurements. The floral characters, between both populations, generally followed similar trends. The juvenile period had a significant *male* GCA_{var} effect in Factorial One, while in Factorial Two, both significant *female* and *male* GCA_{var} effects were reported. In the latter case, the female effect was 3 times its male effect. An unusual result was also found in Factorial Two for its flowering range (FRNG) variable, whereby the replicate effect was highly significant and almost 1.4 times the *female* or *male* GCA_{var} effects. Conversely, the *female* GCA_{var} effect was the prominent feature for FRNG in Factorial One, being almost ~5 times the *male* GCA_{var} effect. The median flowering (MEDF) variable had high significance for all main and interaction effects in both populations. The *female* GCA_{var} effect was respectively, 2.1 and 2.7 times its *male* GCA_{var} effect, as well as having a significant SCA_{var} effect, indicating significant additive and non-additive genetic variation exist for MEDF in both inference base populations (IBP).

The plants showed greater uniformity in MM93 for Factorial One than for Factorial Two for the various treatments (*female*, *male* and *fem*male*) and the between plot variance. This occurred because plants for Factorial Two were of very mixed sizes, in comparison to Factorial One, when plants were grouped at planting. Alternatively, the cumulative (CU96) incremental measurements indicated equal *female* and *male* GCA_{var} effects and a significant SCA_{var} '*fem x male*' for both Factorials.

The significant SCA_{var} effects also suggest hybrid vigour could be responsible for the increased observed variance between plots, particularly in Factorial Two. Although the same vegetative characters are measured in each reference population, a greater number of significant SCA_{var} effects were reported in Factorial Two and also indicate the importance of analysing the two populations separately.

b) Expectations of mean squares for vegetative characters

The internal replication imbalance meant some vegetative characters had less than 6 plants per plot being measured, and that these were then used to estimate the plot mean. As a result, the mean (harmonic) plant numbers per plot varied from 3.89 to 5.91 in Factorial One and 4.11 to 5.87 in Factorial Two (data not shown). The vigour-associated measurements such as trunk diameter (MM93-MM96) and prominent bud counts (PRBD) were obtained from almost every plant (~6 plants per plot). However, the floral attributes were measured from a lesser number of plants (~4 plants per plot), because on average 68% of the total plants were sexually mature across both factorials. In order to calculate the variance component of interest, both the *random* statement and *test* option were used in the GLM analysis. The former provides an estimate of the respective coefficients and these are then pre-multiplied to each variance component of the linear independent mean squares equations. The *test* option overrides the SAS® default *F-test* error term and allows a 'user defined' error term to be specified. These are presented in the v-ratio column of Table III-5. Harmonic weighting adjusts the numerator of the *F-test* with respect to the denominator of the test (Gordon, *pers. comm.*). Consequently, each variable has its own weighting of harmonic means, and therefore, slightly different coefficients (data not shown). The use of these reduced FMD analyses has ensured minimal imbalance in the vegetative characters as evidenced by the weighting factors being close to unity. However, the low numbers of female vines mature in 1996 and their distribution amongst the plots further complicates the fruiting data imbalance problems. Additionally, the low number of seedlings that had crop loads greater than 10 per vine (see Section IV-B - Fruiting data results) further exacerbated the fruit data imbalance problem.

3. Variance component estimation

The preceding section 2 described the partitioning of the variance components and their harmonic mean (weighted) for each expectation of mean squares. The method of variance component estimation and their respective standard errors has been described in Chapter 3 (see Section D.3) for all the vegetative and fruiting data in the FMD study. Accordingly, results for the variance component estimates from the GCA_{var}/SCA_{var} effects are presented here without further explanation. The following tables detail these variance component estimates and their significance from zero.

Table IV-5 : Estimates of the partitioned variance component and their t-test significance from zero.

Factorial One [5x5]						
Variable	σ^2_{blk}	σ^2_{fem}	σ^2_{male}	$\sigma^2_{fem*male}$	$\sigma^2_{error(a)}$	σ^2_{resid}
PRBD	0.3657	0.0551	0.1039	0.0637	0.0997	4.3083 **!
JVPD	0.0045	0.0004	0.0041	0.0018	0.0041	0.2408 **!
MEDF [2]	0.5717	3.4663	1.4655	1.2727	0.1905	11.6209 **!
FRNG	0.7637	3.4629	0.5694	-0.1075 [1]	-0.1516 [1]	21.3156 **!
CU96	0.8969	3.8315	3.2080	0.4975	-1.1524 [1]	27.1521 **!
MM96	0.5401	3.8977	3.4220	0.5644	-0.9965 [1](*)	29.9116 **!
MM95	0.7655	2.3617	1.8559	0.2495	0.0923	20.0421 **!
MM94 [2]	0.1933	0.6611	0.1364	0.0448	0.1983	6.1262 **!
MM93	0.0471	0.0227	0.0227	0.0339	0.1754 **!	1.3635 **!
Factorial Two [6x6]						
Variable	σ^2_{blk}	σ^2_{fem}	σ^2_{male}	$\sigma^2_{fem*male}$	$\sigma^2_{error(a)}$	σ^2_{resid}
PRBD	0.3660	0.0203	0.1709	0.0658	0.0422	3.7557 **
JVPD [2]	0.0092	0.0353	0.0092	0.0086	0.0310 **!	0.2119 **!
MEDF	0.7174	8.3526	2.8456	1.2070 **	0.6389	11.4945
FRNG	0.6555	0.2101	0.3297	0.6705	0.3686	25.7369 **!
CU96	2.3148	4.0559	2.9854	1.5824 *	1.4465 *	28.0918 **!
MM96	4.7786	5.8942	3.0356	2.3413 *	3.3274 **!	32.9603 **!
MM95 [2]	6.9356	4.6814	1.0100	2.0679 (*)	2.9022 **!	23.1514 **!
MM94 [2]	2.7068	1.7826	0.4315	1.1826 (*)	2.2499 **!	8.1609 **
MM93 [2]	0.4834	0.3625	0.0764	0.3256 (*)	0.7679 **!	1.4957 **

Key: F-test significance Pr < 0.001 = **!, Pr < 0.01 = **, Pr < 0.05 = * and Pr < 0.10 = (*).
comp.[1] non-truncated distributions **6 maternal effects** [2] *Factorial One*: FRNG = 6.08 (*); MM94 = 4.85 * Factorial Two: JVPD = 6.08 (*); MM95 = 4.64 ** MM94 = 6.66 **!; MM93 = 4.74 **

The non-significance (from zero) of almost all these estimated components does not preclude their usefulness in determining the various genetical statistics i.e. heritability and genetic correlations. Also included in Table IV-5 is the preferred reporting of the non-truncated (negative) estimates of the distribution for these statistics. There were six vegetative characters that had significant maternal effects (using their respective means squares F-test ratio). These transient maternal effects appeared to dissipate over time i.e. Factorial Two trunk diameter maternal effects had reduced by 1996.

4. Genetical estimates of vegetative characters

a) *Heritability estimates*

The narrow sense heritabilities for the ten vegetative characters can be estimated from the statistics given in the preceding sections 2) and 3). The 'individual plant basis' method, as described in equation II-4 from Hallauer and Miranda (1981), was used for the narrow sense (additive) heritability estimates in the two-factor factorial (RCB). The estimate of heritability due to the non-additive component, has been estimated by substituting the non-additive (interaction) component ($4{*}\sigma^2_{fxm}$) for the additive component ($4{*}\sigma^2_{f\ or\ (m)}$) in the formula of equation II-4. The non-additive heritability, given by Hallauer and Miranda (1981), can be equated to the dominance heritability. Estimates of the non-additive heritability often involved negative or small positive variance components; these negative estimates are included in all estimates used for the FMD study. As previously noted, these variance components are sometimes equated to zero in the literature (Gordon *et al.*, 1972; Searle, 1971). Reporting of these non-truncated estimates can be unsatisfactory, although, in some cases unavoidable, and can lead to a bias in the final estimate. In addition, these heritability estimates are classed as either low if $h^2_n < 0.35$, moderate if $0.35 \leq h^2_n < 0.65$ and high if $h^2_n \geq 065$, in terms of this study.

Table IV-6 : Heritability estimates and approximate standard errors for ten vegetative characters in Factorial One and Two.

h^2 narrow sense heritabilities for vegetative data						
	Factorial One (5x5)			*Factorial Two (6x6)*		
Variable	h^2_{narrow}	±	SE [1]	h^2_{narrow}	±	SE [1]
PRBD	**0.069**	±	0.095	**0.096**	±	0.104
JVPD	**0.036**	±	0.074	**0.301**	±	0.278
MEDF	**0.550**	±	0.548	**0.913**	±	0.757
FRNG	**0.324**	±	0.303	**0.039**	±	0.070
CU96	**0.420**	±	0.397	**0.369**	±	0.338
AGR	**0.396**	±	0.373	**0.355**	±	0.326
MM96	**0.398**	±	0.379	**0.376**	±	0.351
MM95	**0.343**	±	0.330	**0.337**	±	0.328
MM94	**0.223**	±	0.224	**0.321**	±	0.335
MM93	**0.056**	±	0.101	**0.290**	±	0.330

h^2 dominance heritabilities for vegetative data						
	Factorial One (5x5)			*Factorial Two (6x6)*		
Variable	$h^2_{dominance}$	±	SE [1]	$h^2_{dominance}$	±	SE [1]
PRBD	**0.055**	±	0.225	**0.065**	±	0.205
JVPD	**0.029**	±	0.288	**0.116**	±	0.355
MEDF	**0.283**	±	0.561	**0.197**	±	0.335
FRNG	**- 0.017** [2]	±	0.194	**0.098**	±	0.309
CU96	**0.059**	±	0.177	**0.166**	±	0.307
AGR	**0.041**	±	0.154	**0.175**	±	0.303
MM96	**0.061**	±	0.185	**0.197**	±	0.356
MM95	**0.041**	±	0.187	**0.245**	±	0.419
MM94	**0.025**	±	0.196	**0.343**	±	0.571
MM93	**0.084**	±	0.348	**0.430**	±	0.724

[1] from Dickerson's SE (standard error) from Hallauer and Miranda (1981)
[2] reporting of negative estimates for a non-truncated distribution

Narrow sense heritabilities, not surprisingly, reflect the earlier findings from the GCA_{var} effects. Clearly, this is due to the fact that the heritability estimates are based on these GCA_{var} effects. The main feature of these heritabilities is the greater significance in the dominance heritabilities for Factorial Two as compared to Factorial On. In general, both populations showed similar trends in their narrow sense heritabilities, with almost 70% reported as low to moderate for many vegetative characters. However, there were some differences evident in the remaining 30% of these narrow sense heritabilities, which showed the diversity between the two populations. Factorial One had a higher narrow sense heritability for flowering range (FRNG) and a lower narrow sense heritability for juvenile period; the reverse was true in Factorial Two. The vigour measurement heritabilities were very similar, but Factorial Two had more significant dominance effects for these characters. Therefore, it would appear that the dominance and/or epistatic effects was more important in the vegetative characters measured in Factorial Two, as compared to Factorial One. This observation, I believe, further justifies the need for the two reference populations to be analysed separately. In addition, actual *family means* are a prime consideration for plant improvement and selection decisions. Results on a population means basis for these characters exhibit differences in their *basic genetic variation* i.e. between the two populations. Therefore, GCA_{mean} analyses should also be investigated and are subsequently reported here as follows.

b) Combining abilities GCA_{mean} and SCA_{mean}

The method described for estimating GCA_{mean} by male and female is based on Simmonds (1979) and is stated in Chapter 2. The PDIFF (probability of a difference) values were used to discriminate between family GCA performance and these included probabilities of 0.1% to 10% PDIFF levels i.e. $Pr< 0.001$, $Pr< 0.01$, $Pr< 0.05$ and $Pr< 0.10$. The following tables (below) summarise these deviations from their respective population means for 5 selected vegetative characters classified by their parental arrays 'breeding values' i.e. GCA_{mean}. *female* and *male* effects. The PDIFF significance of **all** BiP combinations (being compared), for their GCA breeding values, are not shown here. However, these additional tables would be necessary if any significant SCA_{mean} combinations were to be identified i.e. hybrid vigour.

Table IV-7 : Estimates of GCA_{mean} effects by parental arrays as deviations from the population mean in 5 selected vegetative characters from Factorial One

Vegetative breeding values of GCA_{mean} – by female and male parents						
				Female		
Variable	**mean**	**A**	**B**	**C**	**H**	**M**
PRBD	***8.03***	-0.164	0.480	-0.265	0.178	-0.229
JVPD	***2.55***	0.053	0.052	0.000	-0.076	-0.030
MEDF	***15.01***	1.135 **!	-1.764	-0.620	-1.405	2.650 **!
FRNG	***9.49***	-0.290	-1.750	0.312	-1.173	2.895 **!
CU96	***24.19***	-2.958 **!	-0.427	1.589	-0.262	2.058
				Male		
Variable	**mean**	**01**	**06**	**07**	**09**	**13**
PRBD	***8.03***	-0.314	0.246	0.569	-0.255	-0.246
JVPD	***2.55***	-0.087	0.057	-0.061	0.129	-0.037
MEDF	***15.01***	0.598	-0.001	-1.106	1.980 **!	-1.472
FRNG	***9.49***	1.349 *	-0.543	-0.510	-0.059	-0.236
CU96	***24.19***	0.695	-1.357 *	-2.440 *	1.043	2.058

Key: PDIFF - test probabilities Pr < 0.001 = **!, Pr < 0.01 = **, Pr < 0.05 = * and Pr < 0.10 = (*).

Table IV-8 : Estimates of GCA_{mean} effects by parental arrays as deviations from the population mean in 5 selected vegetative characters from Factorial Two.

Vegetative breeding values of GCA_{mean} – by female and male parents							
				Female			
Variable	**mean**	**F**	**I**	**J**	**K**	**M**	**N**
PRBD	***6.99***	0.062	-0.284	0.362	-0.195	-0.059	0.114
JVPD	***2.27***	-0.323 **!	0.047 **!	-0.131	0.366 **!	0.008	0.003
MEDF	***23.89***	-3.477 **!	-0.746 *	-2.297**!	0.272 *	2.534 **!	3.983 **!
FRNG	***11.62***	-0.529	-0.040	0.015	-0.944	0.941	0.558
CU96	***25.58***	-1.749 **!	1.646	0.962	-3.593 **!	1.576	1.157
				Male			
Variable	**mean**	**03**	**04**	**05**	**08**	**11**	**14**
PRBD	***6.99***	0.804 **!	0.155	-0.213	-0.280	-0.071	-0.394
JVPD	***2.27***	0.152 (*)	-0.061	-0.156 (*)	-0.009	0.010	0.046
MEDF	***23.89***	1.452	1.467	0.723	-2.866 (*)	-1.972 (*)	1.166
FRNG	***11.62***	-0.174	-0.516	1.721 **	-0.626	-0.776	0.372
CU96	***25.58***	1.514	2.367	0.580	-0.748	-0.990	-2.723 **!

Key: PDIFF - test probabilities Pr < 0.001 = **!, Pr < 0.01 = **, Pr < 0.05 = * and Pr < 0.10 = (*).

Results from the GCA_{mean} tables above show distinct and significant differences between each other for their GCA breeding values. Accordingly, the breeding values for JVPD and MEDF characters had significantly higher variation present in the *female* parents from Factorial Two compared to those from Factorial One. The *female* GCA_{mean} effects were significant in 11 out of 30 in Factorial Two, compared to 4 out 25 in Factorial One. In addition, the population means were significantly higher in Factorial Two for MEDF and FRNG as shown in the population comparisons (see Section IV-A).

Conversely, the breeding values of respective *male* parents for all characters showed very similar trends in their effects on variation amongst their respective arrays. The male GCA_{mean} effects were significant in 7 out of 30 in Factorial Two, compared to 4 out 25 in Factorial One for all characters. Certain *male* GCA_{mean} effects were found to be as significant as *female* GCA_{mean} effects for some characters. Therefore 'breeding value' can be very useful in determining the best family (BiP) for either individual selection or as breeding stock. The best *male* GCA_{mean} together with the best *female* GCA_{mean} represent the best BiP for general combining ability (GCA) for a character of interest, when comparing these parental genotypes.

For example, in order to select the best GCA parent that reduces 'juvenile period', the first selection by *female* GCA_{mean} array would indicate female **F** from Factorial Two (GCA_{mean} = -0.323 years). Selection for the best *male* GCA_{mean} array to reduce the juvenile period would indicate male **05** (GCA_{mean} = -0.156 years). Combining these GCA deviations with the grand mean (2.27) gives an expected BiP **F05** mean of 1.79. The observed value for the BiP **F05** mean was 1.76, indicating that a SCA_{mean} effect of -0.061 could have been present. The SCA_{mean} effect for **F05** was tested (amongst its half sib array) and was found to be non-significant at the PDIFF<0.10% (data not shown). Therefore the SCA difference (-0.061) was probably due to either sampling effects from the level of sexual maturity and/or the half sib family size (small) in the population. Clearly then, the advantage of these GCA\SCA_{mean} effects is in their ability to discern between family arrays (GCA) and within families of particular arrays (SCA).

In addition, the JVPD for the **J05** BiP was 1.75 and its SCA_{mean} effect was significant at the PDIFF<0.10%. Therefore, **F05** and **J05** BiP's are successful in reducing JVPD (compared to ALL other BiP's in Factorial Two), the former having the best GCA_{mean} effect while the latter has the best SCA_{mean} effect. Therefore, to distinguish which is the best family **J05** or **F05** to use for reducing JVPD, one could also consider their breeding value for an associated character such as fruit weight. The GCA_{mean} effect of **F05** for fruit weight is far superior to **J05** (see Section IV-B). The **F05** BiP selected as breeding material has two advantages; it reduces the juvenile period and has large fruit size.

5. Phenotypic correlations of vegetative characters

The phenotypic correlations between ten vegetative characters were estimated using Pearson's correlation coefficient in SAS®. Simple correlations of absolute value 0.20 (and higher) can be very useful in biological terms (Harding *et al.,* 1991; Simmonds, 1979). These simple correlations, between two variables, do not adjust for the effects of other variables. However, they are most useful for describing the simple correlation between characters but cannot be used in a predictive manner.

From Table IV-9 (below), almost all trunk vigour measurements (AGR, CU96 and MM93 to MM96) have a simple correlation of 0.20 or higher. It is not surprising to find trunk vigour measurements were highly correlated because they are, in essence, repeated measures over time. However, a curious result was seen for MM93 in Factorial One, which had a r_p = -0.045**ns** when correlated to AGR. This could have been due to the very consistent uniformity of all the plants in Factorial One, at the time of field planting. This observation is also substantiated by the unusually low GCA_{var} results (Table IV-4), Therefore, Table IV-9 should be viewed by excluding the areas with autocorrelations, of the vigour measurements AGR through to MM93 and correlated amongst themselves. These autocorrelations are likely because of the repeated measures nature of the AGR, CU96 and MM93 to MM96 variables. Consequently, the remaining floral characters and trunk vigour measurements in combination with each other can be summarised as follows.

Table IV-9 : Phenotypic simple correlations in ten vegetative characters and their significance from zero from Factorial One (5x5) design and Factorial (6x6) design.

Factorial One 5 x 5 design (RH top diagonal)

	PRBD	JVPD	MEDF	FRNG	AGR	CU96	MM96	MM95	MM94	MM93
PRBD		0.114	-0.027 n.s	-0.089 *	-0.081 *	-0.082 *	-0.105	-0.192	0.200	-0.087 *
JVPD	-0.051 n.s		0.071 n.s	-0.466	-0.111	-0.117	-0.143	-0.243	-0.259	-0.127
MEDF	0.079	0.116		0.298	0.007 n.s	0.019 n.s	0.031 n.s	0.017 n.s	-0.002 n.s	0.048 n.s
FRNG	0.012 n.s	-0.315	0.034 *		0.182	0.179	0.187	0.228	0.169	0.046 n.s
AGR	0.065 n.s	-0.171	-0.025 n.s	0.172		0.981	0.936	0.797	0.540	-0.045 n.s
CU96	0.064 *	-0.132	0.012 n.s	0.190	0.970		0.977	0.842	0.591	0.068 *
MM96	0.054 n.s	-0.105	0.070 *	0.220	0.902	0.970		0.875	0.657	0.273
MM95	-0.015 n.s	-0.087	0.104	0.240	0.746	0.833	0.902		0.774	0.303
MM94	-0.028 n.s	-0.043 n.s	0.148	0.181	0.537	0.641	0.761	0.865		0.430
MM93	-0.033 n.s	0.078 *	0.220	0.135	0.156	0.315	0.536	0.647	0.754	

Factorial Two 6 x 6 design (LH bottom diagonal)

Key - r_p significance's

no mark below r_p then significantly different from zero at Pr≤ 1%,

* these are significantly different from zero at Pr≤ 5%,

n.s these are not significantly different from zero at Pr> 5%

n the number of observations by each variable ranged from

n = *591 - 888* in Factorial One for the ten variables

n = *888 - 1242* in Factorial Two for the ten variables

Table IV-10 : Summary of simple phenotypic correlations in ten vegetative characters (r>0.20).

Correlated variables			Factorial One	Factorial Two
JVPD	*x*	FRNG	-0.466	-0.315
	x	MM95	-0.243	-0.087
	x	MM94	-0.259	-0.043 **ns**
FRNG	*x*	MEDF	0.298	0.034 *
	x	MM96	0.187	0.220
	x	MM95	0.228	0.240
PRBD	*x*	MM94	0.200	-0.028 **ns**
MEDF	*x*	MM93	0.048 **ns**	0.220

All correlations are significantly different from zero i.e. Pr ≤ 1%, unless otherwise stated
* Pr ≤ 5% or **ns** = non-significant

The main features of these phenotypic correlations are summarised above, by considering those correlations with r_p>0.20. The pair-wise comparisons in both IBP's are noted and in these cases at least one (if not both) from the pair of correlations could be significant (r_p>0.20). From these results it is clear that the trends in the phenotypic correlations are very similar between both reference populations, although, there are differences in the correlation of PRBD and vigour measurements, between the two reference populations.

The summary results (Table IV-10) indicate shorter juvenile periods (JVPD) were associated with longer flowering ranges (FRNG), as well as smaller trunk diameters (in 1994 and 1995). The latter association of smaller trunk diameters with JVPD appears to be stronger in Factorial One. In addition, larger trunk diameters in 1995 and 1996 have an associated increase in flowering range in both factorial cases. From these findings it is clear that JVPD can be phenotypic correlated to FRNG and certain other vigour measurements. However, there is no predictive ability in these phenotypic correlations and have limited use outside of describing the phenotypic properties of the IBP's. Therefore, the need to ascertain the genetic correlations seems axiomatic. These genetic correlations would be more informative from the perspective of describing the additive genetic variance and covariance in the IBP's.

6. Genotypic correlations of vegetative characters

Genetic correlations are the correlations between the additive genetic variation (breeding value) of two characters, while the phenotypic (simple) correlations are a linear function of the genetic correlations, environmental correlations and their square root heritabilities (Equation II-13). Falconer (1989) reported that it is possible to have genetic and environmental correlations that are opposite in sign and very different in magnitude, although, the more usual case would be where both correlations are of the same sign and of similar magnitude. The r_a genetic correlations were estimated for the ten vegetative characters of the FMD study. Accordingly, the estimated genetic and phenotypic correlations are presented for the ten vegetative characters in Table IV-11 & Table IV-12. The shaded areas in these tables should be ignored because the correlations are possibly repeated measures or the standard error is twice its mean (in at least one of the factorials).

The analysis of covariance was used in the GLM procedure of SAS® with the associated MANOVA statements. Subsequently, the same expectations used for the mean sum of squares of a single character (see EMS in Table III-5) are also used for the mean sum of cross products between two characters on the same individual. Usually more than one character is measured on individuals (or plots of individuals) during the course of an experiment and these characters are chosen based on their significance to the breeding programme goals and objectives. Consequently selection for X can have either a positive, neutral or negative correlated effect on character Y (unselected). Therefore it is in the plant breeder's interest to ascertain how these correlations manifest and interact between the various key characters. The utility of these genetic correlations is rather more potent than that of the simple phenotypic correlations. The simple phenotypic correlations are useful in a descriptive manner, while the genetic correlations are more robust and can be used in a predictive manner. These genetic and phenotypic correlations are estimated using *partial* correlations from the MANOVA procedure in SAS®. These estimated correlations are based on an adjustment being made for the remaining variables, which requires a full complement of data for all variables being compared. Therefore the error degrees of freedom used in each factorial MANOVA analysis, is further reduced to 437 d.f and 669 d.f, respectively.

Table IV-11 : Genetic [*g*] (±SE) and phenotypic [*p*] (significance from zero) correlations estimated in ten vegetative characters in Factorial One (5x5) design.

		JVPD	MEDF	FRNG	PRBD	CU96	MM96	MM95	MM94	MM93
AGR	*g*	-0.462 *0.368*	0.369 *0.139*	0.624 *0.091*	-1.017 *-0.016*	1.001 *0.000*	0.998 *0.000*	0.979 *0.006*	0.882 *0.066*	0.615 *0.558*
	p	-0.115 **	-0.048 **ns**	0.132 **	-0.006 **ns**	0.989 **	0.965 **	0.770 **	0.510 **	0.015 **ns**
JVPD	*g*		0.263 *0.281*	-0.498 *0.210*	0.009 *0.881*	-0.426 *0.184*	-0.428 *0.178*	-0.354 *0.241*	-0.674 *0.305*	-0.297 *1.539*
	p		0.069 **ns**	-0.480 **	0.036 **ns**	-0.104 *	-0.123 **	-0.226 **	-0.232 **	-0.099 *
MEDF	*g*			0.903 *0.008*	-0.680 *0.070*	0.358 *0.029*	0.338 *0.028*	0.433 *0.033*	0.344 *0.073*	0.009 *0.249*
	p			0.236 **	-0.013 **ns**	-0.040 **ns**	-0.028 **ns**	-0.024 **ns**	-0.011 **ns**	0.052 **ns**
FRNG	*g*				-0.714 *0.059*	0.613 *0.019*	0.612 *0.019*	0.666 *0.021*	0.734 *0.035*	0.392 *0.195*
	p				0.030 **ns**	0.137 **	0.133 **	0.156 **	0.091 *	-0.003 **ns**
PRBD	*g*					-1.015 *-0.003*	-1.009 *-0.002*	-1.065 *-0.016*	-0.752 *0.104*	-0.588 *0.475*
	p					0.011 **ns**	-0.006 **ns**	-0.123 **	-0.180 **	-0.079 **ns**
CU96	*g*						0.997 *0.000*	0.982 *0.001*	0.880 *0.014*	0.611 *0.116*
	p						0.976 **	0.781 **	0.520 **	0.014 **ns**
MM96	*g*							0.992 *0.000*	0.910 *0.010*	0.666 *0.100*
	p							0.814 **	0.596 **	0.233 **
MM95	*g*								0.908 *0.013*	0.742 *0.102*
	p								0.723 **	0.248 **
MM94	*g*									0.415 *0.188*
	p									0.414 **

Error d.f = 437 [*g*] genetic (±SE) and [*p*] partial phenotypic correlations and significance from zero;**ns** non-sign., ' ' no mark; Pr ≤ 10%, * Pr ≤ 5%, ** Pr ≤ 1%

Table IV-12 : Genetic [*g*] (±SE) and phenotypic [*p*] (significance from zero) estimated in ten vegetative characters in Factorial Two (6x6) design.

		JVPD	MEDF	FRNG	PRBD	CU96	MM96	MM95	MM94	MM93
AGR	*g*	0.074 0.916	0.435 0.103	0.245 0.250	0.670 0.305	1.001 0.000	0.971 0.008	0.840 0.049	0.687 0.141	0.483 0.473
	p	-0.147 **	-0.087 *	0.140 **	0.106 **	0.988 **	0.961 **	0.801 **	0.536 **	0.134 **
JVPD	*g*		0.502 0.095	-0.174 0.258	0.258 0.518	0.201 0.136	0.374 0.113	0.521 0.121	0.596 0.173	0.763 0.258
	p		0.012 **ns**	-0.354 **	-0.035 **ns**	-0.148 *	-0.176 **	-0.202 **	-0.218 **	-0.162 *
MEDF	*g*			0.838 0.011	0.243 0.072	0.425 0.016	0.600 0.012	0.755 0.010	0.845 0.015	0.911 0.015
	p			0.007 **ns**	0.030 **ns**	-0.091 **	-0.078 *	-0.071 **ns**	-0.013 **ns**	0.034 **ns**
FRNG	*g*				-0.240 0.151	0.155 0.040	0.158 0.037	0.068 0.048	0.001 0.077	0.110 0.176
	p				0.019 **ns**	0.138 **	0.153 *	0.173 **	0.099 **	0.101 **
PRBD	*g*					0.705 0.043	0.768 0.032	0.863 0.025	0.797 0.059	0.353 0.325
	p					0.118 **	0.115 *	0.074 *	0.038 **ns**	0.015 **ns**
CU96	*g*						0.973 0.001	0.857 0.007	0.710 0.020	0.534 0.068
	p						0.974 **	0.807 **	0.536 **	0.142 **
MM96	*g*							0.949 0.002	0.851 0.011	0.715 0.043
	p							0.859 **	0.638 **	0.361 **
MM95	*g*								0.976 0.002	0.880 0.025
	p								0.742 **	0.436 **
MM94	*g*									0.964 0.013
	p									0.584 **

Error d.f = 669 [*g*] genetic (±SE) and [*p*] partial phenotypic correlations and significance from zero; **ns** non-sign., ‘ ’ no mark; Pr ≤ 10%, * Pr ≤ 5%, ** Pr ≤ 1%

Genetic correlations amongst Factorial One and Factorial Two ranged from -1.065 to 1.001. The phenotypic and genetic correlations (Table IV-11 and Table IV-12) follow very similar trends, for most characters, between both Factorial One and Factorial Two. However, a number of correlations were very different, in both magnitude and direction, these are summarised as follows in Table IV-13. The phenotypic correlations in both factorials are almost identical in direction and magnitude. This finding also suggests that the partial correlations were more effective in determining the 'true' phenotypic correlations. In contrast however, their genetic correlations were of an opposite direction and/or magnitude in certain characters between the two inference base populations. These differences are summarised as follows.

Table IV-13 : Trends in the differences between genetic & phenotypic correlations of Factorial One (3x7) and Factorial Two (3x4) designs.

Variables compared	Correlation	Factorial One	Factorial Two
JVPD versusCU96 &	r_p	small & negative	small & negative
MM93-MM96	r_a	moderate & *negative*	moderate & ***positive***
PRBD versusCU96 &	r_p	small & *negative*	small & ***positive***
MM93-MM96	r_a	*very large* & *negative*	*large* & ***positive***
FRNG versusCU96 &	r_p	small & positive	small & positive
MM93- MM96	r_a	*moderate* & positive	*small* & positive

These genetic correlations can be used to predict the correlated response of a secondary character when selection is applied to a primary or target character. However, to predict the correlated response between two characters several genetical estimates are necessary, these include the

- narrow sense heritability of target and secondary characters
- phenotypic variance of the target character
- selection intensity applied to the target character
- genetic correlation between target and secondary character.

Correlated response in a secondary character can be estimated, given selection is applied to a primary character and is calculated as in equation II-14. Clearly, it is

important to have knowledge of how certain key characters may change when selection is applied to a primary character. Phenotypic correlations are the net effects of the interaction between the plants genetic variation and its environment. The genetic variation being concerned with the heritabilities of the two characters (being correlated) and their respective genetic correlations, while the latter involves their environmental correlations as their complements of heritability (e^2 = 1- h^2), this is termed environmentability (Falconer, 1989).

Investigating the relationships between the phenotypic and genetic correlations can be achieved by focusing on a small number of key attributes simultaneously. Because the primary objective of selection is to improve the *overall mean* of the character toward the desired goal; any negative (correlated) responses of associated characters must be avoided (assuming negative correlated effects are undesirable). Although phenotypic correlations intuitively seem the most useful in a practical sense, they tend to be more of a descriptive statistic. Phenotypic correlations are analogous to broad sense heritability, while in contrast, the genetic correlations are similar to the narrow sense heritability with its predictive application. Genetic correlations, therefore, can be used to estimate the genetic gain from indirect selection. Therefore, it is necessary to understand the genetic correlations between several key characters in order to predict how the complete suite of characters will respond given selection for a primary character. For example, the juvenile period can be effectively selected for in Factorial Two ($\mathbf{h}^2_n$ = 0.301) i.e. to reduce the juvenile period, however, it may be necessary to determine what effect selection for JVPD has on other key characters. Therefore, the reduction in juvenile period of seedlings, although self evident in its benefits, should not deleteriously effect other characters of interest. Accordingly, it would be useful to investigate the correlated response, of selecting for a reduction in juvenile period, with other key character in order to ascertain their correlated effects (see Discussion later).

B. Fruiting data results

1. Fruit characteristics

The descriptive statistics, in Table IV-14 and Table IV-15, shows the of number vines evaluated in 1996 ranged from 105 up to 257, across all nineteen characters measured in both factorials (reduced designs). Although there were some 900 female vines in total across the full FMD, less than half of these vines (40%) had sufficient fruit numbers per vine (>10 fruit) available for evaluation in the 1996 fruiting season. Consequently, vines with >10 fruit available for testing in 1996, was much less than originally expected.

Table IV-14 : Population statistics for nineteen fruiting characters in Factorial One (3x7) reduced design.

Factorial One [3x7]							
Variable	**mean**	**unit**	**±2SE**	**std dev.**	**n**	**min**	**max**
FNO	38.883	**ns**	6.43	51.539	257	0.00	289.00
EBX	7.422	0.001	0.32	2.041	162	5.00	18.00
EDM	17.924	0.001	0.28	1.762	162	14.00	23.00
T6_2	164.600	0.001	1.53	9.730	162	140.40	205.40
D6_2	17.902	0.001	0.28	1.804	162	14.00	23.00
FWT	64.446	0.001	2.62	20.589	247	19.10	136.80
YLD	2.478	**ns**	0.42	3.328	247	0.00	20.00
HVBX	10.024	0.001	0.24	1.422	141	7.40	17.00
HVDM	18.835	0.001	0.47	2.804	141	13.90	28.10
LENM	63.666	**ns**	1.35	10.480	240	33.50	97.50
DMAX	43.079	**ns**	0.68	5.289	240	27.90	59.60
EENDS	1.187	**ns**	0.04	0.291	240	0.63	2.37
EMID1	1.056	**ns**	0.01	0.098	240	0.76	1.42
EMID2	0.997	**ns**	0.00	0.034	240	0.92	1.08
SENBX	14.495	0.001	0.23	1.689	225	10.50	20.00
TEXT	2.594	**ns**	0.09	0.627	214	1.00	5.00
FLAV	2.640	0.001	0.10	0.723	214	1.00	5.00
TAST	10.608	**ns**	0.47	3.460	214	1.00	25.00
STR8	1.896	0.001	0.14	0.852	146	0.20	5.00

Table IV-15 : Population statistics for nineteen fruiting characters in Factorial Two (3x4) reduced design.

Factorial Two [3x4]

Variable	mean	unit	±2SE	std dev.	n	min	max
FNO	48.260	**ns**	6.53	56.226	173	0.00	318.00
EBX	6.446	0.001	0.27	1.590	134	4.20	13.20
EDM	16.109	0.001	0.32	1.826	134	11.50	21.70
T6_2	175.500	0.001	3.73	21.586	134	131.80	262.50
D6_2	16.489	0.001	0.30	1.729	134	12.16	21.45
FWT	71.005	0.001	4.00	26.122	171	17.72	137.00
YLD	3.140	**ns**	0.56	3.644	171	0.02	18.20
HVBX	9.736	0.001	0.24	1.216	105	7.20	12.60
HVDM	17.380	0.001	0.47	2.423	105	11.70	23.40
LENM	62.926	**ns**	1.76	11.266	163	28.59	96.35
DMAX	43.585	**ns**	0.93	5.942	163	28.80	56.32
EENDS	1.130	**ns**	0.06	0.395	163	0.51	3.70
EMID1	1.052	**ns**	0.03	0.187	163	0.78	2.79
EMID2	1.002	**ns**	0.01	0.046	163	0.91	1.15
SENBX	13.968	0.001	0.32	1.887	139	10.00	18.70
TEXT	2.608	**ns**	0.12	0.676	130	1.00	4.00
FLAV	2.446	0.001	0.13	0.727	130	1.00	4.00
TAST	10.485	**ns**	0.63	3.620	130	2.00	19.00
STR8	1.415	0.001	0.19	1.049	124	0.20	6.10

Results showed that nine of the nineteen fruit characters were not significantly different between both data sets. These nine characters included yield, fruit number, shape descriptors and most sensory aspects. However, the remaining ten characters were significantly different, at the 0.1% t-test significance level, on a mean population basis. The precocious flowering behaviour seen earlier in the vegetative results of Factorial One continued at fruiting. The ten day difference reported between Factorials for median flowering date on a population basis, was mimicked by a 10 day difference in the 'time to reach 6.2 %SSC' (T6_2). Therefore, Factorial One was significantly earlier in both flowering and 'time to reach 6.2 %SSC' on a population basis.

Table IV-16 : Trends in the differences between means of nineteen fruiting attributes in Factorial One (3x7) and Factorial One (3x4) reduced designs.

Level of difference	**Variable**	**Factorial One mean (3x7)**	**Factorial Two mean (3x4)**
Large	YLD **ns**	2.478	3.140
	FNO **ns**	38.883	48.260
	EDM	17.924	16.109
	FWT	64.446	71.005
	*T6_2	13 April	23 April
Moderate	STR8	1.896	1.415
	EBX	7.422	6.446
	D6_2	17.902	16.489
	HDM	18.835	17.38
Small	HVBX	10.024	9.736
	SENBX	14.495	13.968
	SHAPE and other sensory scores similar in both cases **ns**		

* converting its numeric value into "days of 1996" [by subtracting the 61 days from the datum November 1 1995] i.e. 175.5 - 61 = 114.5 JD~23 April as described in the Materials and Methods section earlier. **ns** = non-significant

The harvest brix levels (%SSC) were significantly higher than the threshold brix of 8%SSC, indicating that the screening technique was successful in optimising harvest brix. Factorial One was slightly higher for harvest brix than Factorial Two. Generally fruit quality aspects such as flavour, texture and taste scores, along with the various physical attributes of shape, had similar means and variances between both factorial populations. In contrast the productivity characters of fruit number, vine yield and fruit weight were all higher in Factorial Two, but only the latter was statistically significant. Factorial Two had significantly lower 'early dry matter' (EDM). Although this was not unexpected given that these seedlings were generally later flowering as well as being later maturing i.e. higher value for the time to reach 6.2 %SSC. Clearly, significant differences exist between both Factorial designs, for fruit weight and sensory attributes, on a population basis. These results further justify the concurrent and separate analyses of the fruiting data. In summary, Factorial Two generally had larger fruit weight, fruit number and yields per vine as compared to Factorial One. In contrast, Factorial One had significantly earlier maturing fruit with higher dry matter and better storage (after 8 weeks), on a population basis.

2. GLM - ANOVA of fruiting data

a) Combining abilities GCA_{var} and SCA_{var}

The ANOVA tables for the nineteen fruiting characters are presented below. The significance of the *F-test* is calculated using the GLM procedures **user defined** *test* option, in an analogous fashion to the vegetative data analyses. The *F-test* probabilities are derived directly from SAS ®. These synthetic *F-tests* are calculated by using a linear function of mean squares in the denominator (including negative variance components) and a Satterthwaite degree of freedom in the numerator (Littell *et al.,* 1991).

Table IV-17 : Estimated mean squares of nineteen fruit characters and their F-test significance from Factorial One (3x7) design.

Factorial One [3x7] estimated mean squares						
Variable	**block**	**female**	**male**	**fem*male**	**error(a)**	**residual**
FNO	4508.11	15757.64 **	4983.68	2297.98	2846.42	22180.60
EBX	8.52	22.77 **!	14.09 **	2.80	3.83	3.13
EDM	1.02	7.81 *	3.95 **	5.66	2.80	2.94
T6_2	110.97 *	805.76 **	273.63	81.81	52.88	98.00
D6_2	1.44	12.22	3.94	5.77	3.14	2.81
FWT	762.06 *	5072.36 **!	2462.46 **!	144.55	277.06	330.73
YLD	22.03	67.65 **	27.76	9.05	11.13	9.12
HVBX	0.38	11.99 *	1.99	2.25	2.13	1.67
HVDM	5.38	36.48	20.79	9.55	6.52	6.94
LENM	137.56	2485.75 **!	354.07 *	89.96	67.12	87.32
DMAXM	37.98	624.87 **!	165.93 **!	10.27	19.52	17.313
EENDS	10.88	7.06 **	1.79 *	0.54	0.62	0.87
EMID1	0.11	1.86 **!	0.16 *	0.03	0.08	0.08
EMID2	0.24	1.58 **!	0.23	0.09	0.10	0.91
SENBX	5.31	43.89 **!	4.28	2.65	2.75	2.13
TEXT	0.578	2.63	0.79	0.94 **	0.30	0.34
FLAV	0.85	4.58 **!	1.88 **	0.33	0.44	0.45
TAST	19.45	104.75 (*)	29.44	27.26 **	9.13	9.76
STR8	0.53	1.37	2.67 *	0.59	0.68	0.61

Key: F-test probabilities for significance
Pr < 0.001 = **!, Pr < 0.01 = **, Pr < 0.05 = * and Pr < 0.10 = (*).

Table IV-18 : Expected mean squares of nineteen fruit characters and their F-test significance from Factorial Two (3x4) design.

Factorial Two [3x4] estimated mean squares						
Variable	**block**	**female**	**male**	**fem*male**	**error(a)**	**residual**
FNO	1828.88	9088.70 (*)	13971.84 **	2177.29	2809.93	3099.74
EBX	7.56 **	14.95 (*)	31.63 **!	2.40	1.77 *	1.11
EDM	2.16	14.30 *	26.84**	1.19	2.62	2.60
T6_2	496.57	852.22	6846.74 **	115.88	382.72	278.92
D6_2	1.87	11.94 (*)	27.43 **	1.22	2.57	2.19
FWT	386.47	2170.36	15952.91 **	821.76 *	347.34	346.18
YLD	8.00	44.41	115.03 *	12.99	10.22	12.03
HVBX	1.14	1.69	5.13	1.53	1.29	1.36
HVDM	4.24	3.45	50.87 *	5.15	5.64	3.79
LENM	99.09	2481.56 *	1377.03 *	194.99 *	77.33	62.87
DMAXM	10.24	96.99 (*)	711.98 **!	22.71	16.58	20.38
EENDS	0.119	0.724	0.83 (*)	0.217	0.14	0.13
EMID1	0.242	0.182 *	0.22 *	0.02	0.03	0.03
EMID2	0.001	0.005	0.05 **!	0.002 (*)	0.001	0.001
SENBX	2.97	3.49	37.02	1.93	2.87	2.79
TEXT	0.63	1.11	1.48 (*)	0.331	0.49	0.39
FLAV	0.39	4.48 (*)	0.91	0.84 (*)	0.41	0.45
TAST	15.68	51.68 (*)	42.49 (*)	9.80	14.34	10.44
STR8	0.39	10.77 *	1.58	0.52	0.73	1.06

Key: F-test probabilities for significance
Pr < 0.001 = **!, Pr < 0.01 = **, Pr < 0.05 = * and Pr < 0.10 = (*).

The 'blocking' effect was non-significant in almost all characters, suggesting that there was less environmental variation for fruit data as compared to the vegetative data. Factorial One had almost 80% of the fruit characters with significant *female* GCA_{var} effects. In addition to this, 50% of the fruit characters had significant *male* GCA_{var} effects. There was a definite trend for the *female* GCA_{var} effects to be larger in magnitude, than compared to the *male* GCA_{var} effects. These differences in magnitude ranged from 1.5 to 10 times. The only exception to this trend was for storage at week 8 (STR8). Significant SCA_{var} effects were reported for texture (TEX) and taste (TAST), suggesting that some BiP combinations were better tasting than others. The most striking feature about the larger *female* GCA_{var} effects is that it is based only on 3 female levels versus 7 male levels. Therefore, this indicates the 3 female parents are very different, for these fruit characters, while the male parents represent very similar genetic backgrounds

(or allelic frequencies). Table IV-18 summaries the GCA/SCA variance effects for Factorial Two, and these results show the 'blocking' effect was non-significant in all but one character. This indicates that the replicate or 'blocks' was largely ineffective in separating out environmental variance for fruit data (assuming some environmental variation was present). The *screening technique* ensured harvest brix's were above the threshold of 8%SSC. The non-significance of almost every 'source of variation' indicates the *screening technique* was both useful and effective in optimising harvest brix. In direct contrast with Factorial One, the *male* GCA_{var} effects in Factorial Two were greater compared to its female parental effects. The magnitude differences of the *male* GCA_{var} effects also ranged from 1.5 to 10 times larger than the female effects. These results confirm the need for separate analyses of both factorial data sets. Fruit weight (FWT), length (LENM), flavour (FLAV) and 'end to middle 2' (EMID2) all showed significant SCA_{var} effects in Factorial Two, indicating hybrid vigour breeding was at least possible for some characters. Clearly, the males being used in Factorial Two had greater influence on the performance of their female progenies compared to the female parents. This result is an important feature of the FMD study, and illustrates the significance of male parental selection on the fruiting characters of their female offspring.

Significant female and male GCA effects were present for yield in Factorial One; in addition the female component was almost 2.5 times that of the male component. Factorial Two had a significant GCA male effect for yield and this was almost 2.6 times its non-significant female effect. The male effect for yield in Factorial Two again indicates the importance of male parental selection. There were no significant SCA effects reported for yield in either case. The largest range of GCA means for fruit weight and yield was seen in the female effects in Factorial One and in the male effects for Factorial Two. The estimated variance components and their significance from zero were estimated for both factorial data sets. These data are not shown here because in almost every case these estimated components were not significantly different from zero. However, this does not preclude their usefulness in the calculation of the heritabilities of these fruiting characters.

3. Genetical estimates of fruit characters

a) Heritability estimates

The narrow sense (additive) and dominance heritabilities and their approximate standard errors have been estimated. An increased number of negative estimates are reported in the fruiting data. The possible reason for the increase in these negative estimates is due to some confounding at the whole-plot level i.e. error(a). Results from the vegetative ANOVA in both factorials had only four negative variance estimates. However, only one of these was estimated at the 1st order interaction (FxM) effect in Factorial One. Consequently, only the dominance heritability for flowering range (FRNG) was reported as negative. In contrast, almost half the dominance heritabilities for the fruiting data were reported as negative. Clearly, the major difference between the vegetative and fruiting data was the inherent imbalance in the latter. Chapter Three reported the harmonic mean plant numbers (per plot) varied from 1.59 to 2.48 versus 3.89 to 5.91 respectively. Clearly, the increased negative estimates are due in part to the increased imbalance problem. This imbalance results in a larger variance for error(a) as compared to the female by male (FxM) interaction effect, and because the dominance component is estimated by subtracting error(a) from FxM interaction component, it therefore leads to negative estimates. Narrow sense and dominance heritabilities for the nineteen fruit characters measured in the two reduced FMD analyses and are summarised in Table IV-19 and Table IV-20. Heritability for fruit weight was reported as being h^2_n = 0.616 and h^2_n = 1.08 for Factorials One and Two respectively. The reason that the latter value exceeded 1.0 was most likely due to the fact that the additive genetic variance estimate contains up to $^1/_4$ of the non-additive genetic variance. Therefore any significant SCA effect will also be included in the narrow sense heritability estimate, thus inflating its value. Significant SCA effects for fruit weight in Factorial Two, have translated into a significant dominance heritability h^2_{dom} = 0.19 and this substantiates the view expressed above with regard to the overestimate of the additive genetic variance for the narrow sense heritability. Fruit weight heritability values have typically been reported from around 0.6 to 0.8 in most of the kiwifruit literature (Beatson, 1991; Testolin *et al.,* 1995). Heritabilities for yield were low to moderate h^2_n = 0.23 and h^2_n = 0.45 for Factorials One and Two respectively. These low trends in yield heritability are also reported in the

literature (Beatson, 1991; Testolin *et al.,* 1995). The dominance (or SCA effects) heritabilities were non-significant in both cases. Generally, yield has a low to moderate additive genetic variation while mean fruit weight had a high additive genetic basis. Narrow sense heritabilities for Factorial One were low to moderate in almost all cases (~95%), while approximately half of the narrow sense heritabilities were low to moderate for Factorial Two (Table IV-19 and Table IV-20). There were similar trends in the narrow sense heritabilities between both Factorials for the same characters, although there were examples of fruit characters that had very different additive genetic variation (i.e. early dry matter, EDM). Generally, a higher level of additive genetic variation was reported in Factorial Two. Inherent differences in the allelic frequencies of the parental arrays may have led to the differences in these heritabilities. This view is substantiated by the ANOVA summary of main effects for fruiting data in both Factorials. The female parental arrays were more significant in Factorial One, conversely, the male effects were more significant in Factorial Two, indicating that a greater diversity (allelic differences) existed between female lines and male lines respectively. Alternatively, the covariance of relatives' approach may have over estimated the additive genetic component in Factorial Two, because the additive genetic component could be confounded by up to 4 times the $^{1}/_{8}{}^{th}$ epistatic contribution. Certainly, this could have led to the heritability estimates that exceeded 1.0 in fruit weight (FWT), length (LENM) and 'end to middle' (EMID2) in Factorial Two. Generally, the dominance heritabilities (Table IV-20) have 50% low to moderate while the rest are negative estimates. The taste (TAST) and texture (TEXT) characters in Factorial One had significant for SCA_{var} and as a consequence their dominance heritabilities were high but their narrow sense heritabilities were low.

Table IV-19 : Narrow sense heritability estimates and their approximate standard errors for nineteen fruiting characters in Factorials One (3x7) and Two (3x4) designs.

h^2 narrow sense heritabilities for fruiting data						
	Factorial One (3x7)			*Factorial Two (3x4)*		
Variable	$\mathbf{h^2}_{narrow}$	±	SE [1]	$\mathbf{h^2}_{narrow}$	±	SE [1]
FNO	**0.181**	±	0.146	**0.249**	±	0.181
EBX	**0.419**	±	0.293	**0.994**	±	0.691
EDM	**-0.042**	±	0.144[2]	**0.745**	±	0.495
T6_2	**0.466**	±	0.353	**0.969**	±	0.653
D6_2	**0.008**	±	0.179	**0.776**	±	0.515
FWT	**0.616**	±	0.359	**1.080**	±	0.691
YLD	**0.232**	±	0.173	**0.454**	±	0.319
HVBX	**0.181**	±	0.240	**0.238**	±	0.266
HVDM	**0.277**	±	0.279	**0.650**	±	0.486
LENM	**0.665**	±	0.446	**0.898**	±	0.628
DMAXM	**0.847**	±	0.513	**1.061**	±	0.654
EENDS	**0.286**	±	0.201	**0.296**	±	0.253
EMID1	**0.540**	±	0.352	**0.432**	±	0.296
EMID2	**0.400**	±	0.285	**1.157**	±	0.713
SENBX	**0.413**	±	0.306	**0.590**	±	0.378
TEXT	**0.097**	±	0.207	**0.214**	±	0.172
FLAV	**0.421**	±	0.268	**0.214**	±	0.249
TAST	**0.194**	±	0.252	**0.254**	±	0.198
STR8	**0.315**	±	0.239	**0.510**	±	0.401

[1] from Dickerson's SE (standard error) from Hallauer and Miranda (1981)
[2] reporting of negative estimates for a non-truncated distribution

Table IV-20 : Dominance heritability estimates and their approximate standard errors for nineteen fruiting characters in Factorials One (3x7) and Two (3x4) designs.

h^2 dominance heritabilities for fruiting data						
	Factorial One (3x7)			*Factorial Two (3x4)*		
Variable	h^2_{narrow}	±	SE [1]	h^2_{narrow}	±	SE [1]
FNO	**-0.103**	±	0.135[2]	**-0.092**	±	0.138[2]
EBX	**-0.155**	±	0.175[2]	**0.105**	±	0.238
EDM	**0.501**	±	0.385	**-0.227**	±	0.129[2]
T6_2	**0.161**	±	0.196	**-0.243**	±	0.097[2]
D6_2	**0.432**	±	0.395	**-0.228**	±	0.137[2]
FWT	**-0.130**	±	0.063[2]	**0.191**	±	0.191
YLD	**-0.094**	±	0.133[2]	**0.049**	±	0.178
HVBX	**0.021**	±	0.293	**0.095**	±	0.366
HVDM	**0.232**	±	0.312	**-0.057**	±	0.274[2]
LENM	**0.055**	±	0.119	**0.283**	±	0.272
DMAXM	**-0.131**	±	0.065[2]	**0.044**	±	0.117
EENDS	**-0.057**	±	0.104[2]	**0.147**	±	0.267
EMID1	**-0.213**	±	0.062[2]	**-0.119**	±	0.148[2]
EMID2	**-0.068**	±	0.127[2]	**0.106**	±	0.127
SENBX	**-0.047**	±	0.153[2]	**-0.118**	±	0.124[2]
TEXT	**0.624**	±	0.401	**-0.179**	±	0.190[2]
FLAV	**-0.118**	±	0.119[2]	**0.312**	±	0.370
TAST	**0.577**	±	0.380	**-0.180**	±	0.194[2]
STR8	**-0.087**	±	0.224[2]	**-0.133**	±	0.184[2]

[1] from Dickerson's SE (standard error) from Hallauer and Miranda (1981)
[2] reporting of negative estimates for a non-truncated distribution

b) Combining abilities GCA_{mean} and SCA_{mean}

The PDIFF significance test could not be estimated on the least squares means (LSM) fruiting data, because of the severe female vine imbalance at the whole-plot level. Consequently, the parental array mean deviations are reported here without any significance probabilities. However, the trends in these mean deviations are still useful, especially given any significant *F-test* for their GCA_{var}/SCA_{var} effects. The fruit weight *F-test* in Factorial One was significant for both male and female effects. From the GCA_{mean} table below, female M has a large positive effect on fruit number and a small positive effect on fruit weight; both characters combining to increase yield. Clearly, the M female has significant general combining ability (GCA) for these productivity attributes in Factorial One.

Table IV-21 : Estimates of GCA_{mean} effects by female parental arrays as deviations from the population mean in 19 selected fruit characters from Factorial One 3x7.

Fruit data breeding values GCA_{mean} – by female parents				
			Female	
Variable	**mean**	**C**	**H**	**M**
FNO	***38.88***	-3.93	**-10.61**	**14.54**
EBX	***7.42***	0.46	0.31	-0.77
EDM	***17.92***	0.59	-0.30	-0.30
T6_2	***164.61***	-1.00	-3.17	4.17
D6_2	***17.90***	0.68	-0.23	-0.45
FWT	***64.45***	**7.46**	**-11.05**	3.58
YLD	***2.48***	0.01	**-0.9**	**0.88**
HVBX	***10.02***	0.28	0.27	-0.55
HVDM	***18.84***	1.06	-0.17	-0.88
LENM	***63.67***	-1.46	-4.91	6.36
DMAXM	***43.08***	3.29	-2.22	-1.07
EENDS	***1.19***	-0.01	0.10	-0.09
EMID1	***1.06***	-0.03	0.06	-0.03
EMID2	***0.99***	0.00	0.02	-0.01
SENBX	***14.49***	0.87	-0.30	-0.56
TEXT	***2.59***	0.21	-0.07	-0.14
FLAV	***2.64***	0.31	-0.13	-0.17
TAST	***10.61***	**1.34**	-0.48	**-0.87**
STR8	***1.89***	-0.07	0.23	-0.16

Table IV-22 : Estimates of GCA_{mean} effects by male parental arrays as deviations from the population mean in 19 selected fruit characters from Factorial One 3x7.

Fruit data breeding values GCA_{mean} – by male parents								
					Male			
Variable	**mean**	**01**	**02**	**06**	**07**	**09**	**12**	**13**
FNO	***38.88***	0.23	**18.23**	-8.34	**-16.38**	5.92	6.23	-5.89
EBX	***7.42***	-0.09	-0.24	1.33	1.21	-0.64	-0.82	-0.75
EDM	***17.92***	-0.22	0.13	0.44	0.34	-0.44	0.25	-0.50
T6_2	***164.61***	0.60	0.88	-3.73	-3.90	0.60	5.80	-0.25
D6_2	***17.90***	-0.08	0.12	0.59	0.33	-0.40	0.04	-0.61
FWT	***64.45***	-2.06	6.26	0.94	-4.46	**14.81**	-2.97	**-12.52**
YLD	***2.48***	0.80	**1.01**	-0.76	**-0.94**	0.59	0.14	*-0.84*
HVBX	***10.02***	0.16	0.17	0.14	-0.01	0.23	-0.06	-0.63
HVDM	***18.84***	0.23	-0.41	1.04	1.96	-0.91	-0.42	-1.48
LENM	***63.67***	1.31	5.98	-1.40	-3.57	0.80	-0.66	-2.47
DMAX	***43.08***	-0.47	-0.08	1.62	-0.31	4.10	-1.45	-3.41
EENDS	***1.19***	-0.06	-0.04	-0.08	0.14	0.00	0.01	0.02
EMID1	***1.06***	-0.03	-0.02	-0.01	0.01	0.00	0.02	0.03
EMID2	***0.99***	-0.01	0.00	0.01	0.00	-0.01	0.00	0.00
SENBX	***14.49***	0.21	-0.11	0.13	-0.15	0.11	-0.08	-0.12
TEXT	***2.59***	0.28	-0.11	-0.01	-0.14	0.12	0.03	-0.19
FLAV	***2.64***	0.33	0.05	0.00	-0.33	0.17	-0.06	-0.16
TAST	***10.61***	**1.76**	-0.48	-0.03	-1.01	0.76	0.10	**-1.09**
STR8	***1.89***	-0.42	-0.19	-0.04	0.15	-0.27	-0.05	0.82

Productivity attributes were improved by the use of male 02 in a similar manner to that described for the female M effect. Therefore it is possible that the best BiP combination from Factorial One for productivity could be M02. However, it is important to note that the sensory attributes for both parents M and 02 are small and negative, resulting in vines that have better than average yields but less than average (inferior) fruit quality. The use of the GCA means tables can indicate the best families to use in future breeding for a combination of characters. Information about the amount of additive genetic variation (narrow sense heritability) and more importantly the genetic correlation between these combinations of characters must also be considered.

Table IV-23 : Estimates of GCA_{mean} effects by female parental arrays as deviations from the population mean in 19 selected fruit characters from Factorial Two 3x4.

Fruit data breeding values GCA_{mean} – by female parents				
			Female	
Variable	**mean**	**I**	**M**	**N**
FNO	***48.26***	**-11.10**	**8.41**	2.69
EBX	***6.44***	-0.24	-0.36	0.60
EDM	***16.11***	0.45	0.27	-0.71
T6_2	***175.50***	1.60	2.60	-4.20
D6_2	***16.49***	0.56	0.04	-0.60
FWT	***71.01***	**6.83**	0.98	**-7.81**
YLD	***3.14***	**-0.50**	**0.78**	-0.27
HVBX	***9.74***	0.18	-0.06	-0.12
HVDM	***17.38***	0.28	-0.22	-0.06
LENM	***62.93***	1.82	6.63	-8.45
DMAXM	***43.59***	1.55	-0.82	-0.73
EENDS	***1.13***	0.00	0.10	-0.10
EMID1	***1.05***	0.04	0.02	-0.06
EMID2	***1.00***	0.01	0.00	-0.01
SENBX	***13.97***	0.25	0.02	-0.27
TEXT	***2.61***	0.17	-0.06	-0.11
FLAV	***2.44***	**0.28**	0.13	**-0.41**
TAST	***10.49***	1.11	-0.15	-0.95
STR8	***1.42***	0.23	0.35	-0.58

The GCA_{mean} effects for the reduced FMD 3x4 in Factorial Two also reveals the M female as having good general combining ability for improving productivity. In addition, the M female (in BiP combination) with the 05 male could result in the best overall increase in yield. Although, the best GCA mean effect for fruit weight was from male 08, its negative GCA effect for fruit number actually resulted in a lower than average yield for the array. The mean deviations by male effects are in agreement with the variance based results whereby the male effects were very significant in the GLM-ANOVA and also had a greater influence in the range of mean deviations as compared to the female arrays. This illustrates the usefulness of both the GCA variance results and the GCA means tables in describing the respective inference base populations.

Table IV-24 : Estimates of GCA_{mean} effects by male parental arrays as deviations from the population mean in 19 selected fruit characters from Factorial Two 3x4.

Fruit data breeding values GCA_{mean} – by male parents					
		Male			
Variabl	**mean**	**03**	**05**	**08**	**11**
FNO	***48.26***	4.16	**22.49**	-6.54	**-20.11**
EBX	***6.44***	-0.30	-1.30	0.42	1.18
EDM	***16.11***	-0.97	-0.51	-0.19	1.67
T6_2	***175.50***	-1.51	19.00	-6.36	-11.13
D6_2	***16.49***	-1.14	-0.29	-0.18	1.61
FWT	***71.01***	-18.48	12.49	**24.57**	**-18.58**
YLD	***3.14***	-0.66	**2.10**	0.24	**-1.68**
HVBX	***9.74***	-0.27	-0.23	0.03	0.48
HVDM	***17.38***	-1.67	-0.60	-0.17	2.43
LENM	***62.93***	-6.72	4.68	6.73	-4.70
DMAX	***43.59***	-3.34	2.90	5.26	-4.82
EENDS	***1.13***	0.07	0.16	-0.08	-0.14
EMID1	***1.05***	0.01	0.09	-0.05	-0.06
EMID2	***1.00***	-0.01	0.04	-0.03	-0.01
SENBX	***13.97***	-0.83	-0.17	-0.56	1.56
TEXT	***2.61***	-0.30	0.19	0.12	-0.02
FLAV	***2.44***	-0.17	0.07	-0.07	0.16
TAST	***10.49***	**-1.66**	**1.03**	0.55	0.08
STR8	***1.42***	-0.16	0.15	-0.26	0.27

The most striking feature from the GCA mean table above, for male arrays in Factorial Two, was the contrast of male 05 and male 11 for fruit number. The former has a 22 fruit number increase on average, while the latter has a reduction in fruit number by a similar amount. The range being almost as large as the mean itself at 42.60 *versus* 48.26, simply by selecting a high 'fruit number' GCA male *versus* a low 'fruit number' GCA male. However, the next most intriguing aspect from this difference in fruit number GCA, is the fact that male 11 also reduces the average fruit weight and consequently yield. Contrasting with this, the 05 male has both increased fruit number and average fruit weight that leads to improved yields. Therefore, it is necessary to investigate the phenotypic and genetic correlations between various key fruiting characters.

4. Phenotypic correlations of fruiting characters

The simple phenotypic correlations amongst nineteen fruiting characters for both Factorials One and Two are listed in the following from Table IV-25 to Table IV-29. From these tables it is evident that there are 171 combinations are available amongst these nineteen fruiting characters. However, there are certain combinations that must be excluded from the discussion of these results, because they are either related (mathematically) or are repeated measures of the same character. Because many of these correlations are likely to be autocorrelated, therefore, some or all of these variables are less useful in the present FMD study. These can be grouped into the following four categories :

EBX, HVBX, T6_2 and their *three* combinations

EDM, HVDM, D6_2 and their *three* combinations

EENDS, EMID1, EMID2 and their *three* combinations

TAST with FLAV or TEXT and their *two* combinations

As a result, 11 correlations can be ignored due to similarities in their measurements, which leaves 160 combinations amongst the nineteen fruiting characters. Correlations of 0.2 (absolute value) or higher, were considered 'biologically' significant and using this threshold level, there were 40 and 48 respective combinations, from Factorials and Two, reported to be 0.20 or higher. These correlations ranged from -0.577 to +0.938 in Factorial One and -0.477 to +0.901 in Factorial Two. Generally, several correlations exhibited similar trends between both the data sets for fruiting characters, although there were also some distinct differences between certain correlations. These differences involve certain combinations of characters compared across each factorial. There are 22 comparisons between the same combinations, in each Factorial, that are considered to be different in either their direction or magnitude. These are summarised as follows.

Table IV-25 : Summary of simple phenotypic correlations in nineteen fruiting characters in Factorial One (3x7) design and Factorial Two (3x4) design.

Factorial One 3 x 7 design – phenotypic correlations

	FNO	EBX	EDM	T6_2	D6_2	FWT	YLD	HVBX	HVDM	LEN
DMAX	-0.057 ns	-0.065 ns	-0.157 ns	0.124 ns	-0.120 ns	0.799	0.097 ns	-0.051 ns	-0.119 ns	0.294
EENDS	-0.019 ns	-0.037 ns	-0.119 ns	-0.083 ns	-0.104 ns	0.168	-0.013 ns	-0.082 ns	-0.142 ns	-0.204
EMID1	0.005	-0.019	-0.186	-0.027	-0.144	-0.157	-0.003	-0.039	-0.145	-0.090
EMID2	0.030 ns	-0.011 ns	-0.167 *	0.047 ns	-0.143 ns	0.042 ns	0.055 ns	0.009 ns	-0.142 ns	0.052 ns
SENBX	-0.136 *	0.347	0.709	-0.352	0.743	-0.028 ns	-0.110 ns	0.444	0.629	-0.164 *
TEXT	0.027 ns	-0.016 ns	0.019 ns	0.00 ns	0.055 ns	0.136 *	0.057 ns	-0.087 ns	0.019 ns	-0.042 ns
FLAV	-0.030 ns	-0.034 ns	0.079 ns	-0.056 ns	0.146 ns	0.179	0.009 ns	-0.019 ns	0.051 ns	0.043 ns
TAST	0.019 ns	-0.021 ns	0.032 ns	-0.010 ns	0.076 ns	0.161 *	0.053 ns	-0.083 ns	0.026 ns	-0.029 ns
STR8	0.002 ns	0.009 ns	-0.043 ns	0.048 ns	-0.055 ns	-0.189 *	-0.106 ns	-0.183 *	0.128 ns	-0.143 ns

Key - r_p significance's
no mark below r_p then significantly different from zero at Pr≤ 1%,
* these are significantly different from zero at Pr≤ 5%,
n.s these are not significantly different from zero at Pr> 5%

n the number of observations by each variable ranged from
n = *146 - 257* in Factorial One for the ten variables
n = *105 - 171* in Factorial Two for the ten variables

Table IV-26 : Summary of simple phenotypic correlations in nineteen fruiting characters in Factorial One (3x7) design.

Factorial One 3 x 7 design - phenotypic correlations (RH top diagonal)

	FNO	EBX	EDM	T6_2	D6_2	FWT	YLD	HVBX	HVDM	LEN
FNO		0.198 *	-0.012 ns	0.168 *	-0.075 ns	-0.001 ns	0.938	-0.185 *	-0.067 ns	0.137 *
EBX	-0.153 ns		0.527	-0.678	0.533	-0.219	-0.264	0.481	0.739	-0.342
EDM	-0.098 ns	0.413		-0.417	0.934	-0.234	-0.041 ns	0.419	0.783	-0.201 *
T6_2	-0.304	-0.678	-0.417		-0.444	0.229	0.240	-0.358	-0.577	0.349
D6_2	-0.094 ns	0.338 *	0.931	-0.370		-0.211	-0.104 ns	0.472	0.814	-0.211
FWT	-0.067 ns	-0.140 ns	-0.046 ns	0.186 *	-0.011 ns		0.164	-0.145 ns	-0.271	0.680
YLD	0.901	-0.245	-0.110 ns	0.389	-0.087 ns	0.167 *		-0.208 *	-0.116 ns	0.264
HVBX	0.082 ns	0.211 *	0.300	-0.114 ns	0.342 ns	-0.062 ns	0.017 ns		0.507	-0.302
HVDM	-0.048 ns	0.595	0.743	-0.477	0.784	-0.147 ns	-0.114 ns	-0.343		-0.385
LEN	0.022 ns	-0.160 ns	0.158 ns	0.177 *	0.151 ns	0.729	0.147 ns	0.012 ns	0.022 ns	

Factorial Two 3 x 4 design - phenotypic correlations (LH bottom diagonal)

Key - r_p significance's **n** the number of observations by each variable ranged from n = *146 - 257* in Factorial One for the ten variables

n = *105 - 171* in Factorial Two for the ten variables

no mark below r_p then significantly different from zero at Pr≤ 1%,

* these are significantly different from zero at Pr≤ 5%,

n.s these are not significantly different from zero at Pr> 5%

Table IV-*27* : Summary of simple phenotypic correlations in nineteen fruiting characters in Factorial Two (3x4) design.

Factorial Two 3 x 4 design – phenotypic correlations

	FNO	EBX	EDM	T6_2	D6_2	FWT	YLD	HVBX	HVDM	LEN
DMAX	0.004 ns	-0.156 ns	-0.079 ns	0.263	-0.068 ns	0.826	0.198 *	-0.099 ns	-0.182 ns	0.392
EENDS	0.007 ns	-0.325	-0.121 ns	0.265	-0.122 ns	0.112 ns	0.030 ns	0.034 ns	-0.178 ns	0.149 ns
EMID1	0.047 ns	-0.363	-0.066 ns	0.327	-0.058 ns	0.160 *	0.079 ns	-0.061 ns	-0.114 ns	0.218
EMID2	0.185 *	-0.419	-0.097 ns	0.498	-0.039 ns	0.188 *	0.241	-0.040 ns	-0.064 ns	0.143 ns
SENBX	-0.112 ns	0.224 *	0.739	-0.291	0.737	-0.209 *	-0.111 ns	0.287	0.546	-0.050 ns
TEXT	-0.176 *	-0.116 ns	0.095 ns	-0.000 ns	0.117 ns	0.302	-0.126 ns	0.099 ns	0.036 ns	0.179 *
FLAV	-0.145 ns	0.004 ns	0.345	-0.081 ns	0.333	0.048 ns	-0.085 ns	0.219 *	0.220 *	0.243
TAST	-0.193 *	-0.108 ns	0.154 ns	-0.015 ns	0.172 ns	0.292	-0.134 ns	0.134 ns	0.080 ns	0.216 *
STR8	-0.007 ns	0.035 ns	0.314	0.133 ns	0.133 ns	0.014 ns	0.075 ns	-0.159 ns	0.295	0.172 ns

Key - r_p significance's
no mark below r_p then significantly different from zero at Pr≤ 1%,
* these are significantly different from zero at Pr≤ 5%,

n the number of observations by each variable ranged from n = *146 - 257* in Factorial One for the ten variables
n = *105 - 171* in Factorial Two for the ten variables
n.s these are not significantly different from zero at Pr> 5%

Table IV-28 : Summary of simple phenotypic correlations in nineteen fruiting characters in Factorial One (3x7) design and Factorial Two (3x4) design.

Factorial One 3 x 7 design (RH top diagonal)									
DMAX	**EENDS**	**EMID1**	**EMID2**	**SENBX**	**TEXT**	**FLAV**	**TAST**	**STR8**	
	-0.059 **ns**	0.116 **ns**	0.089 **ns**	0.093 **ns**	0.154 *	0.276	0.197	-0.134	**DMAX**
-0.049 **ns**		0.678	0.308	-0.068 **ns**	0.028 **ns**	-0.076 **ns**	0.009 **ns**	0.015 **ns**	**EENDS**
-0.027 **ns**	0.830		0.736	-0.144 *	-0.020 **ns**	-0.151 *	-0.049 **ns**	0.059 **ns**	**EMID1**
0.192 *	0.416	0.558		-0.173	-0.076 **ns**	-0.198	-0.109 **ns**	0.022 **ns**	**EMID2**
-0.233	-0.100 **ns**	-0.037 **ns**	-0.016 **ns**		0.151 *	0.451	0.231	-0.045 **ns**	**SENBX**
0.331	-0.075 **ns**	0.069 **ns**	0.029 **ns**	0.037 **ns**		0.359	0.981	-0.159 *	**TEXT**
0.021 **ns**	0.061 **ns**	0.061 **ns**	0.108 **ns**	0.476	0.232		0.535	-0.257	**FLAV**
0.313	-0.058 **ns**	-0.058 **ns**	-0.049 **ns**	0.130 **ns**	0.981	0.418		-0.191 *	**TAST**
0.033 **ns**	0.072 **ns**	0.072 **ns**	0.205 *	0.176 **ns**	-0.006 **ns**	0.147 **ns**	0.022 **ns**		**STR8**
Factorial Two 3 x 4 design (LH bottom diagonal)									

Key - r_p significance's **n** the number of observations by each variable from n = *146 - 257* in Factorial One for the ten variables
no mark below r_p then significantly different from zero at Pr≤ 1%, n = *105 -171* in Factorial Two for the ten variables
* these are significantly different from zero at Pr≤ 5%, **n.s** these are not significantly different from zero at Pr> 5%

Table IV-29 : Summary of differences between certain simple phenotypic correlations in fruiting characters (*r*>0.20 in at least one case).

Correlated variables			Factorial One	Factorial Two
EBX	x	EENDS	-0.037 **ns**	-0.325
		EMID1	-0.019 **ns**	-0.363
		EMID2	-0.011 **ns**	-0.419
T6_2	x	EENDS	-0.083 **ns**	0.265
		EMID1	-0.027 **ns**	0.327
		EMID2	0.047 **ns**	0.498
		DMAX	0.124 **ns**	0.263
LEN	x	EDM	-0.201	0.158 **ns**
		HVBX	-0.302	0.012 **ns**
		HVDM	-0.385	0.022 **ns**
		FLAV	0.043 **ns**	0.243
		TAST	-0.029 **ns**	0.216*
		EMID1	-0.090 **ns**	0.149 **ns**
		EMID2	0.052 **ns**	0.218
FLAV	x	EDM	0.079 **ns**	0.345
		D6_2	0.146 **ns**	0.333
		HVBX	-0.019	0.219*
		HVDM	0.051 **ns**	0.220*
STR8	x	EDM	-0.043 **ns**	0.216*
		HVDM	0.128 **ns**	0.295
		FLAV	-0.257	0.147 **ns**
		EMID2	0.022 **ns**	0.205
YLD	x	HVBX	-0.208	0.017 **ns**

Shape parameters (EENDS, EMID1 and EMID2) are moderately and negatively correlated with the EBX character in Factorial Two. This trend suggests increases in EBX (early season fruit) are associated with particular fruit shape parameters. In a similar fashion, any increases in T6_2 (late season fruit) have a correlated increase in their shape measurements. Both characters, EBX & T6_2, indicate earliness in fruit season and in both cases there is a trend for particular shaped fruit to be associated with early season fruit in Factorial Two. However this is not the trend in Factorial One. The flavour component FLAV of fruit from Factorial Two, increases with increasing EDM, D6_2, HVBX and HVDM; these correlations ranged from 0.219 to 0.345. Although these correlations are statistical very weak they are useful in describing the phenotypic properties of these reference populations.

Additionally, there is a phenotypic correlation between EDM, HVBX and HVDM for LEN, in Factorial One, albeit a moderate and negative one. These main features of the simple phenotypic correlations serve a very useful purpose of describing the properties of these various characters and their correlations amongst each other. Generally, these results indicate the diversity between Factorial One and Factorial Two for the various correlations between these nineteen fruiting characters.

5. Genotypic correlations of fruiting characters

Genetic correlations and their standard errors for twelve selected fruiting characters are reported in tables a and b. These genetic correlations range from -1.187 to +0.915 in Factorial One and -1.282 to +1.176 in Factorial Two. Although, in both factorial cases I have avoided using genetic correlations from the following combinations.

- TAST versus all other characters, because the TAST variable is simply a mathematical derivation of FLAV and TEXT (see Materials and Methods).
- Shape measurements EENDS, EMID1, EMID2 and correlations amongst themselves because they are essentially repeated measurements of fruit widths and therefore are expected to be well correlated with each other;
- any reported correlations with standard errors in excess of twice the estimated genetic correlation.

These groups can possibly be well correlated amongst themselves because of the nature of their estimates i.e. as either repeated measures or the fact that they are simply mathematical variants of the same data. Therefore, of the 66 genetic and phenotypic (partial) correlations, in each factorial data set, only 53 combinations are useful for discussion (this excludes the above correlations from TAST etc). There were a number of genetic and phenotypic correlations that were very high (and were in the same direction) between both factorials. These results have been summarised in the following tables.

Table IV-30 : Summary of genetic [g] (±SE) and phenotypic [p] correlations estimated nineteen fruiting characters in Factorial One (3x7) design.

	FWT		YLD		SENBX		TEXT		FLAV		TAST		LENM		DMAX		EENDS		EMID1		EMID2		
g	-0.248	0.001	0.661	0.010	-0.801	0.006	-0.558	0.040	-1.187	-0.022	-1.187	-0.004	-0.636	0.001	-0.060	0.003	0.303	0.028	-0.281	0.050	-0.021	0.049	**FNO**
p	-0.144	ns	0.908	**	-0.011	ns	-0.121	ns	-0.026	ns	-0.121	ns	-0.118	ns	-0.131	ns	-0.016	ns	-0.016	ns	0.030	ns	
g			0.605	0.008	-0.453	0.009	0.915	0.007	-0.688	0.021	1.378	-0.007	0.763	0.001	0.769	0.001	0.313	0.021	0.489	0.031	0.243	0.035	**FWT**
p			0.081	ns	-0.092	ns	0.053	ns	-0.050	ns	0.041	ns	0.696	**	0.784	**	-0.546	ns	-0.047	ns	0.065	ns	
g					-0.928	0.038	0.239	0.971	-0.608	0.605	0.086	0.174	0.095	0.030	0.583	0.037	0.600	0.355	0.215	0.928	0.353	0.767	**YLD**
p					-0.009	ns	-0.199	ns	-0.029	ns	-0.197	ns	0.092	ns	0.030	ns	-0.080	ns	-0.019	ns	0.031	ns	
g							0.070	0.930	0.612	0.545	0.325	0.142	-0.035	0.027	-0.420	0.042	-0.637	0.299	-0.324	0.791	0.030	0.795	**SENBX**
p							-0.007	ns	0.469	**	0.089	ns	-0.066	ns	-0.077	ns	0.062	ns	-0.024	ns	0.062	ns	
g									0.849	1.137	1.643	-2.305	0.771	0.089	0.668	0.206	-0.132	5.015	0.474	3.821	0.578	2.801	**TEXT**
p									0.100	ns	0.979	**	0.109	ns	0.150	ns	-0.022	ns	-0.114	ns	-0.156	ns	
g											1.501	-0.755	0.836	0.029	0.158	0.161	0.211	2.168	0.634	1.309	0.370	1.613	**FLAV**
p											0.299	*	0.070	ns	-0.051	ns	0.191	ns	0.095	ns	-0.011	ns	
g													-0.989	0.001	1.623	-0.090	-0.570	0.512	-1.027	-0.040	-0.753	0.271	**TAST**
p													0.119	ns	0.119	ns	0.018	ns	-0.090	ns	-0.152	ns	
g															0.442	0.007	0.560	0.084	0.592	0.077	0.179	0.098	**LENM**
p															0.327	*	0.013	ns	0.055	ns	0.001	ns	
g																	0.161	0.202	0.316	0.181	0.170	0.166	**DMAX**
p																	-0.249	*	-0.302	*	0.065	ns	
g																			0.847	0.777	0.708	1.170	**EENDS**
p																			0.838	**	0.295	*	
g																					0.870	0.552	**EMID1**
p																					0.430	**	

Error d.f = 67 [*g*] genetic (±SE) and [*p*] partial phenotypic correlations & their significance from zero **ns** non-sign.; Pr ≤ 10%, * Pr ≤ 5%, ** Pr ≤ 1%.

Table IV-31 : Summary of Genetic [g] (±SE) and phenotypic [p] correlations estimated nineteen fruiting characters in Factorial Two (3x4) design.

	FWT		YLD		SENBX		TEXT		FLAV		TAST		LENM		DMAX		EENDS		EMID1		EMID2		
g	0.649	0.045	0.300	0.672	-0.490	0.901	-0.829	1.934	-0.289	2.515	-0.603	0.583	1.176	-0.057	-0.206	0.241	-1.282	-2.222	-0.805	1.173	-0.965	0.197	**FNO**
p	-0.172		0.954	**	-0.163		0.070	ns	-0.045	ns	0.056	ns	-0.063	ns	-0.105	ns	0.036	ns	0.129	ns	0.150	ns	
g			0.727	0.006	0.409	0.018	0.571	0.077	0.522	0.037	0.506	0.013	0.478	0.002	0.763	0.002	-0.506	0.048	-0.769	0.025	-0.731	0.025	**FWT**
p			-0.048	ns	-0.296	**	0.050	ns	0.000	ns	0.046	ns	0.735	**	0.792	**	-0.038	ns	0.043	ns	0.232	*	
g					-0.174	0.204	-0.268	1.015	0.008	0.486	-0.167	0.158	1.051	-0.003	0.024	0.045	-1.230	-0.313	-0.904	0.107	-0.955	0.044	**YLD**
p					-0.162	*	0.059	ns	-0.018	ns	0.051	ns	0.045	ns	0.017	ns	0.055	ns	0.155	ns	0.207	*	
g							1.704	-3.339	1.063	-0.102	1.372	-0.230	-0.483	0.032	0.927	0.010	0.039	0.978	-0.381	0.809	-0.230	0.765	**SENBX**
p							-0.003	ns	0.370	**	0.075	ns	-0.289	*	-0.215	*	-0.048	ns	-0.042	ns	-0.176		
g									1.485	-4.901	1.046	-0.128	-0.778	0.087	1.361	-0.317	-0.238	4.815	-0.695	2.549	-0.750	1.838	**TEXT**
p									0.210	*	0.978	**	0.023	ns	-0.065	ns	-0.003	ns	-0.079	ns	-0.107	ns	
g											1.217	-0.290	-0.280	0.090	0.860	0.043	-0.136	2.226	-0.389	1.859	-0.308	1.692	**FLAV**
p											0.408	**	0.019	ns	0.023	ns	-0.059	ns	-0.065	ns	-0.100	ns	
g													-0.569	0.022	1.099	-0.011	-0.189	0.731	-0.546	0.514	-0.559	0.430	**TAST**
p													0.023	ns	-0.055	ns	-0.016	ns	-0.088	ns	-0.121	ns	
g															-0.194	0.009	-0.829	0.038	-0.659	0.067	-0.717	0.049	**LENM**
p															0.436	**	-0.025		0.142	ns	0.254	**	
g																	-0.037	0.208	-0.469	0.157	-0.392	0.145	**DMAX**
p																	0.056	ns	0.072	ns	0.222	*	
g																			0.829	0.859	0.828	0.738	**EENDS**
p																			0.706	**	0.314	**	
g																					0.926	0.324	**EMID1**
p																					0.703	**	

Error d.f = 109 [*g*] genetic (±SE) and [*p*] partial phenotypic correlations & their significance from zero **ns** non-sign.; Pr ≤ 10%, * Pr ≤ 5%, ** Pr ≤ 1%.

Table IV-32 : Trends in the genetic & phenotypic correlations between fruiting characters from Factorial One 3x7 and Factorial Two 3x4.

Correlated variables				**Factorial One**	**Factorial Two**
FNO	vs	YLD	r_p	0.954	0.908
			r_a	0.300 **ns**	0.661
FWT	vs	LEN	r_p	0.735	0.696
			r_a	0.478	0.763
	vs	DMAX	r_p	0.792	0.784
			r_a	0.763	0.769
SENBX	vs	FLAV	r_p	0.370	0.469
			r_a	1.063	0.612
	vs	LEN	r_p	-0.289	-0.035
			r_a	-0.483	-0.066 **ns**

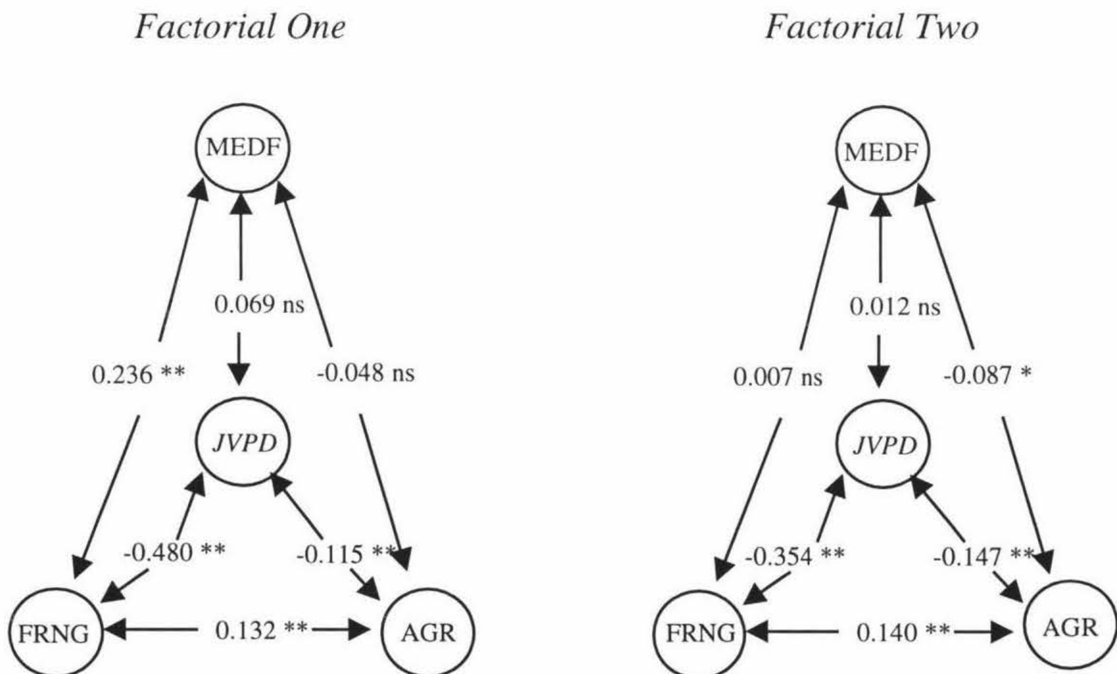
These particular correlations have moderate to high phenotypic and genotypic correlations, although it is not surprising given the inter-relatedness between some of these characters. For example, it is self evident that increased fruit number should also correlate with increased yields, and that increased fruit weight should be associated with increased fruit length and/or fruit diameter. However, in the case of SENBX sensory brix (%SSC of ripe fruit) versus flavour (FLAV) there is a very strong genetic correlation between these two characters, while the phenotypic correlations are moderate at best. In addition, it should be emphasised that restrictions due to the low number of female parents being sampled (three in both factorials) and the very low degree of freedom in each case, 109 and 67 respectively, will limit the usefulness of these correlations. Fruit quality is measured by several key attributes and in this FMD study, the most important of these are (in rank order); fruit weight (FWT), flavour (FLAV), sensory brix (SENBX) and yield (YLD). As a consequence of the high additive genetic basis of fruit weight, direct selection (using individual selection) and is expected to yield a reasonable response (R), in both factorial designs. Assuming these genetic correlations (above) are reasonable, the plant breeder can estimate the response in the key attributes when correlated to the direct improvement of fruit weight. Therefore, the correlated response in the flavour, sensory brix and yield can be predicted (see later in Discussion section).

C. Discussion of Results

Several selection strategies can be investigated for improving the *A.deliciosa* germplasm based on the results from the FMD study. The nature of genetic variation for characters of interest (high or low additive variation) and their genetic correlation with other important characters must be considered. Consequently, applying selection for a single character and evaluating its direct response can be estimated. In addition, the correlated response of an indirect character (not selected for) can also be estimated. This is particularly important if the indirect character's response is not in the desired direction. The following two-dimensional pyramids illustrate the phenotypic and genetic correlations between key floral characters and growth rate (see Figure IV-1 below). This will be followed by a similar discussion with regard to other key fruit characters.

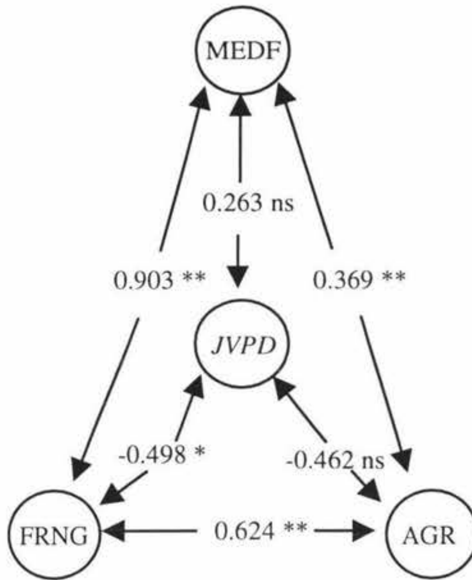
Figure IV-1 : Phenotypic and genetic correlations between various floral characters and growth rates in Factorial One (5x5) and Factorial Two (6x6) designs.

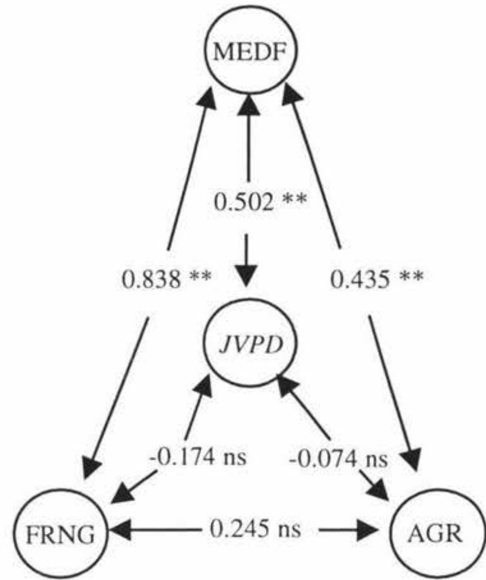
Phenotypic correlations



Genetic correlations

Factorial One *Factorial Two*





Reducing the juvenile period (JVPD) by selection and its correlated effects on other characters (AGR, MEDF and FRNG).

Phenotypic correlations between four vegetative characters

Phenotypic correlations amongst the four characters (see pyramids Figure IV-1) are similar in magnitude and direction, for both Factorials One and Two, with the exception of the median flowering (MEDF) to flowering range (FRNG) case. In comparing the MEDF to FRNG correlation; Factorial One had a r_p = 0.236 and Factorial Two was almost zero, r_p = 0.007 **ns**. In addition, Factorial One showed an increase in MEDF was associated with an increase in its FRNG, phenotypically at least. In contrast, however, both Factorials reported their strongest correlation was for flowering range (FRNG) with the juvenile period (JVPD). In both cases the effect was moderate in size and negative in direction. Therefore, shorter juvenile periods were phenotypically correlated with longer flowering ranges. Phenotypic correlations are very useful in describing the association of various characters particularly in a retrospective manner, however, they cannot be effectively used to predict the change in r_p due to selection.

Consequently, genetic correlations between specific pairwise combinations of characters is necessary, in order to predict the change (correlated response) in the unselected character, due to selection of a primary or target character.

Genetic correlations between four vegetative characters

Trends in the genetic correlations are similar in both factorials, for the four characters. Although, the genetic correlation of AGR to JVPD is moderate (in size) and negative for Factorial One $r_a = -0.462$ while Factorial Two is close to zero, $r_a = 0.074$ **ns**. In addition, the genetic correlation of AGR to FRNG in Factorial One is three times the r_a of Factorial Two. Clearly, there are larger differences in these genetic correlations even though there are similarities in their respective phenotypic correlations. As a further example, let us consider individual selection to reduce the juvenile period in each Factorial separately. The expected response or genetic gain should be different in each case because the genetic variation between both factorials is also very different (see Section IV-A.4). The following example is based on selecting five of the most precocious females and five of the most precocious males i.e. proportion = 0.0176. These individuals are then crossed (i.e. as BiP's). Their progenies are expected to have a population average close to the calculated predicted gain.

Factorial One 5x5 design

25	full sib families
36	seedlings per family
900	Total seedlings
567	number sexually mature (63%)
5	selecting 5 most precocious females
5	selecting 5 most precocious males
10	
0.0176	selected proportion
2.480	selection intensity (from Becker, 1992)

Direct selection for reducing JVPD in Factorial One

$h^2_{n\,JVPD} = 0.036$ $\qquad \sigma_{A\,JVPD} = 0.0954$

$\overline{X}_{JVPD} = 2.554$ $\qquad i = -2.480$

$$R = -(2.480)\left(\sqrt{0.036}\right)(0.0954)$$

$$= -0.0449$$

$$\overline{X}_{selcn} = 2.554 - 0.0449$$

$$= \mathbf{2.509}$$

Indirect selection for JVPD by selecting FRNG in Factorial One

The above example for direct (mass) selection uses a selection intensity of –2.480 because the selection truncation is on the left-hand side of the distribution (i.e. reducing JVPD) and is therefore negative. However, when using correlated response for selecting FRNG, here the selection intensity is on the right hand side of the distribution and is +2.480. But the important point is that the genetic correlation between JVPD and FRNG is actually negative, therefore resulting in a reduction to the mean JVPD.

Correlated response in the juvenile period from direct selection for flowering range is described below and assumes the same selection intensity (2.480) is used on flowering range as that which was used in the direct selection for JVPD, given above. The flowering range (FRNG) was chosen because it has low to moderate heritability and a moderate negative genetic correlation with JVPD.

$h^2_{n\,JVPD} = 0.036$ $h^2_{n\,FRNG} = 0.324$ $r_{a\,(JVPDvsFRNG)} = -0.498$

$i = 2.480$ $\sigma_{A\,JVPD} = 0.0954$ $= 2.554$

$$CR = (2.480)(\sqrt{0.324})(-0.498)(0.0954)$$
$$= |\,0.0671\,|$$
$$\overline{X}_{JVPD} = 2.554$$
$$\overline{X}_{selcn} = 2.554 - 0.0671$$
$$= \mathbf{2.487}$$

Relative selection efficiency (R.S.E.) of direct selection versus indirect selection for JVPD in Factorial One

The relative selection efficiency (R.S.E.) of direct selection versus indirect selection (assuming the same selection intensity applied to both characters) can be estimated as

$$\frac{CR}{R} = \frac{|0.0671|}{0.0449} = 1.494$$

Alternatively, the genetic correlation between the two characters JVPD and FRNG and their respective square root heritabilities also gives the same result as follows

$$\frac{r_a h_{FRNG}}{h_{JVPD}} = \frac{-0.498\left(\sqrt{0.324}\right)}{\sqrt{0.036}}$$

$$= \left|1.494\right|$$

Therefore, it is (-)49.4% more efficient to select for FRNG to reduce the JVPD in Factorial One. The negative value of the *R.S.E* simply indicates the direction of the genetic gain from indirect (mass) selection of FRNG. This result confirms the fact that the low additive genetic variation basis of JVPD, in Factorial One, renders itself less effective for individual selection compared to indirect selection of FRNG. This is a result of the FRNG variable having a higher additive genetic variation (heritability) and a moderate negative genetic correlation with JVPD.

Therefore it is important to consider genetic correlations and correlated responses between key characters in order to maximise response. In order to simulate the 'same' conditions in Factorial Two, a number of assumptions were used. In the example for Factorial Two, the character median flowering date (MEDF) was used instead of flowering range (FRNG) because the former had a higher narrow sense heritability and also a higher genetic correlation with JVPD.

The selection intensity in the previous example JVPD in Factorial One (above), is the same as that used in the calculations (below) for JVPD in Factorial Two. This was made possible by modifying the number of parents selected both male and females as 16 (out of 946) and 10 (out of 569) respectively, giving a selected proportion of approximately 0.17, in both cases.

Factorial Two 6x6 design

36	full sib families
36	seedlings per family
1296	Total seedlings
946	number sexually mature (73%)
8	selecting 8 most precocious females
8	selecting 8 most precocious males
16	
0.017	selected proportion
2.480	selection intensity (from Becker, 1992)

Direct selection for reducing JVPD in Factorial Two

$h^2_{n\,JVPD}$ = 0.301 $\sigma_{A\,JVPD}$ = 0.2986

$\overline{X}_{JVPD}$ = 2.276 i = -2.480

$$R = -(2.480)(\sqrt{0.301})(0.2986)$$
$$= -0.406$$

$$\overline{X}_{selcn} = 2.276 - 0.406$$
$$= \mathbf{1.87}$$

Indirect selection for JVPD by selecting MEDF in Factorial Two

$h^2_{n\,JVPD}$ = 0.301 $h^2_{n\,MEDF}$ = 0.913 r_a = 0.502

i = -2.480 $\sigma_{A\,JVPD}$ = 0.2986 $\overline{X}_{JVPD}$ = 2.276

$$CR = (2.48)(\sqrt{0.913})(-0.502)(0.2986)$$
$$= -0.3552$$
$$\overline{X}_{selcn} = 2.276 - 0.3552$$
$$= \mathbf{1.921}$$

Also the relative selection efficiency (R.S.E.) can be given by -

$$\frac{CR}{R} = \frac{0.3552}{0.406} = 0.875$$

Relative selection efficiency (R.S.E.) of direct selection versus indirect selection for JVPD in Factorial Two

Indirect selection of MEDF on the LHS of the truncation means the intensity of selection (i) is negative i.e. to reduce the MEDF period. From the estimates above, the indirect selection for juvenile period in Factorial Two, is 87.5% as efficient when compared to direct selection. Consequently, genetic gain would be best achieved by direct selection for juvenile period in Factorial Two. In contrast, the reduction in juvenile period in Factorial One is best selected for by using indirect selection for flowering range (FRNG). An important feature about these results is that even though the phenotypic correlations were very similar between both factorials; it is in fact the genetic variation (heritabilities) and their respective genetic correlations that determine the correlated

responses between these key characters. Therefore, the correlated response estimates between various characters of interest should be ascertained. From which an understanding of these correlated effects could potentially avoid the situation whereby selection for one character might adversely effect the progress of an indirect character. This issue will be raised again in considering the correlations between the fruiting characters in the following section. The mass selection strategy was the only strategy considered in these examples. It would of course be possible to estimate the family and combined selection strategies response from direct selection, although, these calculations were not included here. However, the narrow sense heritabilities used in the following example are similar to (but not exactly the same as) those quoted earlier in Table IV-20 and IV-21. The reason for this being the MANOVA procedure in Proc GLM uses a much reduced degree of freedom for the residual errors 109 d.f & 67 d.f respectively. These are much less than those used in the estimates of the complete data sets. However, even with these restrictions it is still possible to estimate the correlated response of these associated characters given direct selection for fruit weight. For illustrative purposes the pyramid style diagrams will be used again here.

Figure IV-2 : Phenotypic correlations between various fruiting characters in Factorial One (3x7) and Factorial Two (3x4) designs.

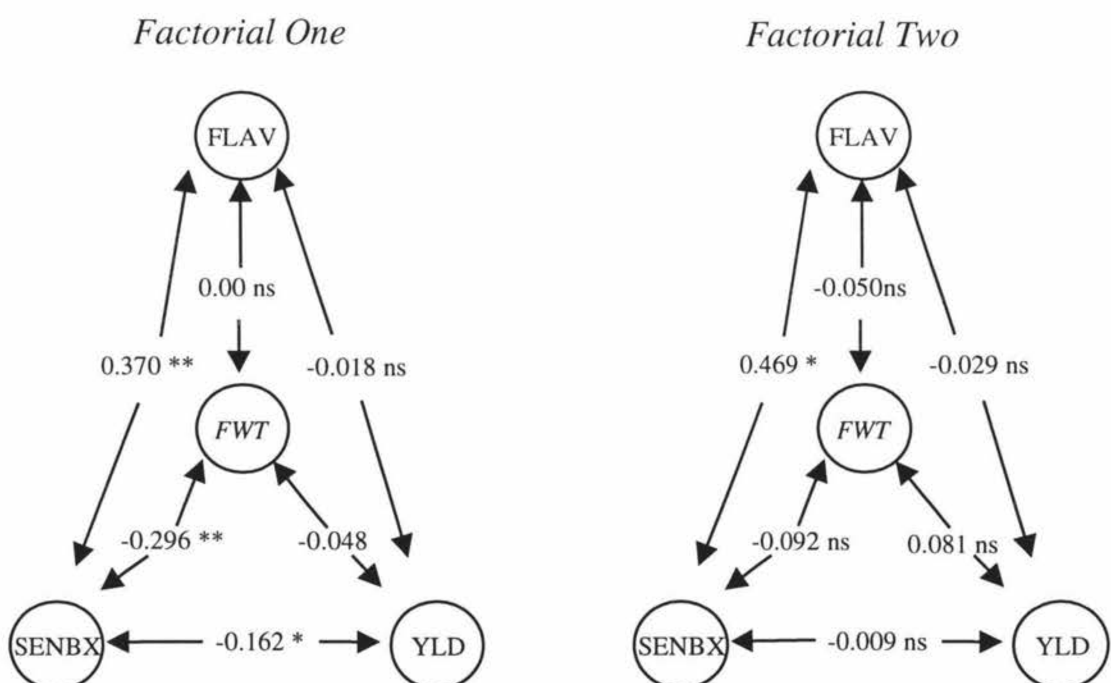
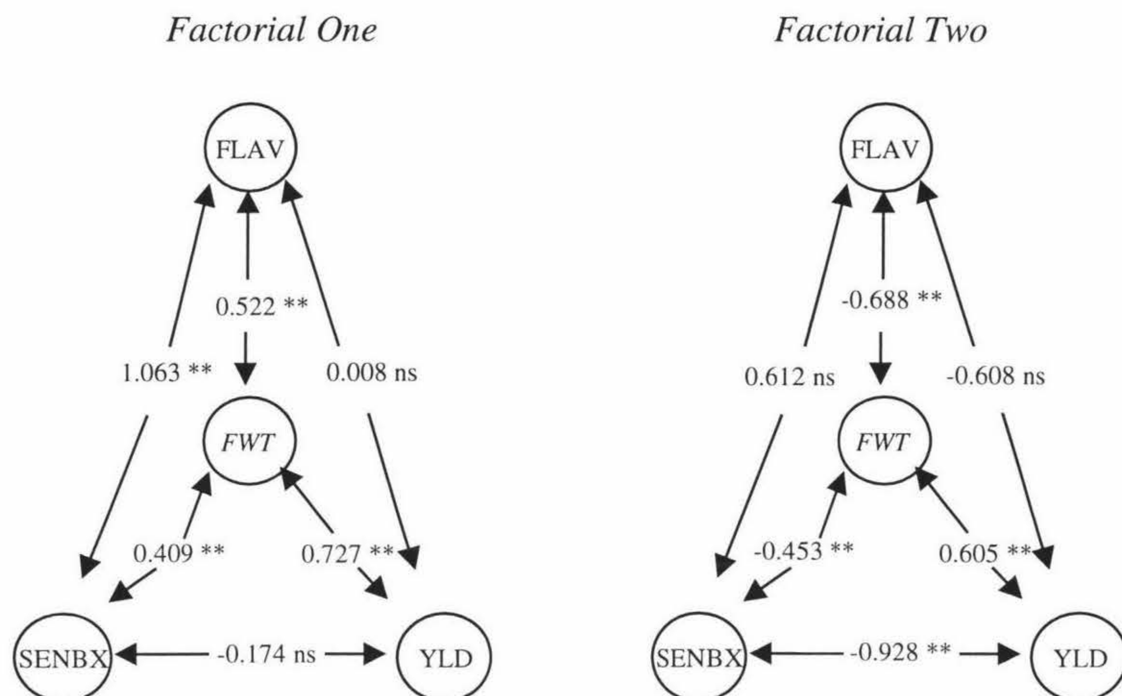


Figure IV-3 : Genetic correlations between various fruiting characters in Factorial One (3x7) and Factorial Two (3x4) designs.



Increasing fruit weight (FWT) by direct selection versus its correlated effects on other characters (FLAV, SEN and YLD).

Phenotypic correlations amongst four fruiting characters

Phenotypic correlations of four fruiting characters show similarities between both Factorials One and Two. The most significant correlation, in both cases, being sensory brix (SEN) versus flavour (FLAV), a weak correlation existed between sensory brix (SEN) and fruit weight (FWT), in Factorial One this suggests bigger fruit were associated with lower sensory brix, albeit a weak correlation.

Genetic correlations amongst four fruiting characters

The trends amongst these correlations were different in three out of the six correlations, these can be summarised as follows:

Correlated variables			**Factorial One**	**Factorial Two**
FWT	vs	SEN	positive & moderate	*negative* & moderate
FWT	vs	FLAV	positive & moderate	*negative* & high
YLD	vs	FLAV	**ns**	*negative* & moderate

Clearly, the contrasting genetic correlations would tend to indicate that very different correlated responses are inevitable if the fruit weight is selected for in each case. The following scenarios will investigate these possibilities. The genetic correlation between fruit weight and flavour has contrasting effects for Factorial One and Two. There is a negative genetic correlation in Factorial One, but a positive effect in Factorial Two. However, in both cases the genetic variation is moderate to high for fruit weight and low to moderate for flavour. Selection for fruit weight is a key objective in the population improvement of the *A. deliciosa* programme. Therefore, direct selection can be successfully used to increase fruit weight in both factorial designs. However, the correlated response in fruit flavour by selecting for increased fruit weight should be considered, in order to determine the correlated response in fruit flavour. For example, the following calculations describe the expected response for direct selection of fruit weight and its correlated response in flavour for each Factorial One and Two separately.

Scenario One:

Factorial One 3 x 7 design

21	full sib families
36	seedlings per family
756	total seedlings
476	number sexually mature (~ 63%)
210	number females assessed
2	selecting the 2 best fruit weight females
2	selecting the 2 best fruit bud weight males
4	
0.0095	selected proportion
2.375	selection intensity (from Becker, 1992)

Direct selection for increasing FWT in Factorial One

$h^2_{n\,FWT}$ = 0.616 $\sigma_{A\,FWT}$ = 16.127

$\overline{X}_{FWT}$ = 64.5 i = 2.372

$$R = 2.375\left(\sqrt{0.616}\right)16.127$$

$$= 30.06$$

$$= 64.5 + 30.06$$

$$\overline{X}_{selcn} = \mathbf{94.56}$$

Correlated response in FLAV by selecting FWT in Factorial One

The following example illustrates the correlated response in flavour (FLAV) given direct selection has been applied for fruit weight (as above).

$h^2_{n\,FWT}$ =	0.616	$h^2_{n\,FLAV}$ =	0.421	$r_{a\,(FWTvsFLAV)}$ =	0.522
i =	2.375	$\sigma_{A\,FLAV}$ =	0.7392	$\overline{X}_{FLAV}$ =	2.6

$$CR = 2.375\left(\sqrt{0.616}\right)(0.522)0.7392$$
$$= 0.7193$$

$$R_{FLAV} = 2.6 + 0.719$$
$$= \mathbf{3.319}$$

Therefore, direct selection for fruit weight in Factorial One has a positive correlated response in it's flavour score. Therefore, improving fruit weight by mass (phenotypic) selection has the associated increase in fruit quality or flavour. In contrast, Factorial Two has a very different result for the flavour score given direct selection for fruit weight as follows.

Scenario Two

Factorial Two 3 x 4 design

12	full sib families
36	seedlings per family
432	total seedlings
315	number sexually mature (~ 73%)
127	number females assessed
1	selecting best female for fruit weight
1	selecting best male for bud weight
2	
0.0157	selected proportion
2.411	selection intensity (from Becker, 1992)

Scenario Two

Factorial Two 3 x 4 design

$h^2_{n\,FWT}$ = 1.08 $\qquad \sigma_{A\,FWT}$ = 28.24

$\overline{X}_{FWT}$ = 71.01 $\qquad i$ = 2.411

$$R = 2.411\left(\sqrt{1.08}\right)28.24$$
$$= 70.76$$
$$= 71.01 + 70.76$$
$$\overline{X}_{selcn} = \mathbf{141.77}$$

It is important to recognise these estimates are based on identifying the best males (to use as parents) for fruit weight, although, males (strictly) do not have fruit. Therefore, sib selection for males from the families with the biggest female fruit weight can be used. In addition, the phenotypic bud size of each male, could be an indicator of possible effects on fruit weight, can be used to separate males in the best families. However, these calculations are based on selecting both the best male and female for FWT, from each Factorial separately. Therefore, the failure to apply selection pressure to the male parental line will in fact reduce the genetic gain by a half. However, for illustrative purposes we will assume the plant breeder is able to effectively select for the male parents.

Correlated response in FLAV by selecting FWT in Factorial Two

$h^2_{n\,FWT}$ = 1.08 $\qquad h^2_{n\,FLAV}$ = 0.214 $\qquad r_{a\,(FWTvsFLAV)}$ = -0.688

i = 2.411 $\qquad \sigma_{A\,FLAV}$ = 0.749 $\qquad \overline{X}_{FLAV}$ = 2.5

$$CR = 2.41\left(\sqrt{1.08}\right)\left(-0.688\right)0.749$$
$$= -0.947$$

$$R_{FLAV} = 2.5 + - 0.947$$
$$= \mathbf{1.209}$$

The mean fruit weight is expected to increase from direct selection for fruit weight in Factorial Two, with a correlated reduction in its flavour score. This is in contrast to the expected results in Factorial One, whereby increased fruit weight was also associated with an increase in its flavour score.

Considering the Flavour response from direct selection versus its correlated response (with fruit weight) in both factorial designs

If selection pressure was applied directly for flavour (alone) then response would be 0.738 and –0.386 for Factorial One and Two respectively. These direct responses can be compared to the correlated response from selecting for fruit weight (above). The relative selection efficiency (RSE) would result in the correlated response being 63.1% (less efficient) in Factorial One and -1.547 or -54.7% (more efficient but causing a reduction), in Factorial Two. Clearly, there are complexities involved with the character's heritability, genetic correlations and their relationships to predicted gain. Therefore, these associations should be investigated before deciding which selection strategy to use and in order to achieve an overall improvement of the key characters desired in a new cultivar. Generally, this result shows that some type of selection index should be developed for selection of a suite of characters considered important in the breeding of *A.deliciosa* (beyond the scope of this study).

D. Conclusions and Recommendations

1. Conclusions

Results from both vegetative and fruiting data has shown high phenotypic and genetic variation is present in the 1991 *A.deliciosa* germplasm of the New Zealand Kiwifruit Breeding programme. Significant additive genetic variation exists for many key characters. There is also an indication that some characters have significant dominance genetic variation, thus suggesting hybrid vigour breeding is possible for at least some characters. Vegetative and fruiting characters with high additive genetic variation are readily improved by individual phenotypic selection. The wider germplasm base used in the FMD study has provided various genetical estimates, which pertain to the inference base (target) population of the 1991 *A.deliciosa* germplasm. The experimental design used in the 1996 Factorial Mating Design study (FMD) suffered from a number of biological constraints, that led to an imbalance in some of the data. There were three major reasons for these imbalance problems

1) crossing failures of certain BiP's led to a lower number of seedlings being planted than was anticipated.

2) an overall low sexual maturity (~68% sexually mature).

3) low fruit numbers per vine (many vines with less than 10 fruit) and a female to male ratio of 1:1.32, resulting in less females than was expected in 1996.

These factors were further exacerbated by the distribution amongst plots of the female vines, resulting in some plots with no females. The latter point was found to be due to the plot size of 6 plants per plot being too small. This problem could have been partially overcome by the use of a larger plot size i.e. 9 plants per plot. Therefore, the fruiting data analyses in the FMD study are less robust as compared to the vegetative data, because of the greater restrictions imposed on it. As a consequence of these biological constraints, the fruiting data analyses were completed on a much-reduced number of parental genotypes.

Therefore much of the genetical estimates should be considered preliminary at best. However, it is hoped that any of these findings will be confirmed by further data collection over future years (1997 & 1998) from more mature vines in a SPLIT plot in time analysis. It is self evident that the female parents must be considered very important for their gametic contribution towards their female F_1 offspring performance, especially for their fruiting characteristics. However, the results presented here in the FMD study strongly suggest the male parents contribution towards their female F_1 offspring performance is as equally potent. The most convincing evidence for this was the exceptional GCA effect of the male parents (in particular "05") on the fruit number, weight and vine yield of their female F_1 offspring. Because the male parents' genes for these fruiting characteristics are not readily "visible" i.e. they do not manifest in the 'strictly classified' male itself, and there has been a tendency for the breeding lines to be somewhat focused on female only selections. Although, the male parents contribution towards their female F_1 offspring performance has been significant (in the FMD results) there is the problem that these male parents must be tested first. Certainly, it would be very advantageous to identify the breeding value of the male parents for a specific character of interest and this is generally termed male progeny testing. Many of the genetical statistics are similar in some instances to those previously reported on a much narrower germplasm (Zhu, 1990; Beatson, 1991). Therefore, certain characters such as fruit weight, fruit length and fruit maximum diameter, could be considered "universally" (within the *A.deliciosa* germplasm) moderate to high for narrow sense heritability. However, other characters such as yield, fruit number and fruit quality aspects (flavour, texture and taste) are almost always moderate to low for narrow sense heritability. The implications of which are that improving fruit quality (flavour, taste etc.) will be more difficult than improving productivity attributes i.e. fruit weight.

2. Recommendations

The most critical finding from the 1996 FMD study has been the problems of imbalance at the whole plot level for female vines. This design 'flaw', of low to no female vines in some plots has led to a compromising of the data analyses particularly for the fruiting data. Therefore, I would recommend that future genetical designs, using the planting of both male and female vines, should be done with a plot size that ensures at least one female (by chance) per plot. From the FMD study results the increase of plot size from 6 to 9 would have alleviated the female vine imbalance to some extent. In addition, the establishment of a concurrent parent's offspring trial (POR) in order to ascertain the genetic contributions at the whole plot level (i.e. genetic fraction) for various characters would also be necessary. The upper limits for narrow sense heritability could also be estimated from the parent off-spring method. More information is required before any decisions can be made with respect to the best families or individuals, to use with any selection strategy. However, early indications suggest Factorial Two has higher productivity and later maturing fruit as compared to Factorial One. In addition, the most significant male from Factorial Two for fruit weight, number and yield is male '05', and this could be used in several new second generation crosses with known females from the Factorial Two data set. For example the best fruit weight and the most precocious family mean from the complete data set of Factorial Two 6x7 full design is F05 cross (data not shown). Therefore selecting the best individual female for fruit weight from the F05 line and using a full-sib set of crosses to the known males from this family should produce large precocious F2 lines. Clearly, it is very important to ensure the field design is optimised in order to achieve the most from the Factorial Mating Design (FMD). Future kiwifruit experimental designs should attempt to plant a full set of seedlings in the field and to avoid unbalanced designs such as the current FMD study. Finally, from these preliminary results it is recommended that the data from 1996, 1997 and 1998 be combined and analysed in order to either confirm or refute any of these early findings.

V. Appendices

1. Appendix A : List of reference tables

Table V-1 : Factorial One and Two gender flowering summaries for 1995, 1996 detailed by block and sub-total by factorial.

BLK	FACT.	% male.	% fem.	% mature	% imm.	F:M ratio	male	female	imm.	No.plnts
1995 Flowering data										
35	1	34.9%	27.9%	62.8%	37.2%	1.3	391	312	417	**1120**
40	1	37.5%	26.6%	64.0%	36.0%	1.4	199	141	191	**531**
Sub-totals		*35.7%*	*27.4%*	*63.2%*	*36.8%*	*1.3*	590	453	608	**1651**
40	2	45.2%	32.9%	78.0%	22.0%	1.4	220	160	107	**487**
46	2	42.9%	30.3%	73.2%	26.8%	1.4	210	148	131	**489**
47	2	37.3%	30.6%	67.9%	32.1%	1.2	180	148	155	**483**
Sub-totals		*41.8%*	*31.3%*	*73.1%*	*26.9%*	*1.3*	610	456	393	**1459**
Totals Factorial One & Two		**38.6%**	**29.2%**	**67.8%**	**32.2%**	**1.3**	1200	909	1001	**3110**
1996 Flowering data										
BLK	**FACT.**	**% male.**	**% fem.**	**% mature**	**% imm.**	**F:M ratio**	**male**	**female**	**immat.**	**No.plnts**
35	1	44.9%	43.4%	88.4%	11.6%	1.0	502	485	130	**1117**
40	1	47.3%	42.9%	90.2%	9.8%	1.1	251	228	52	**531**
Sub-totals		45.7%	43.3%	89.0%	11.0%	1.1	753	713	182	**1648**
40	2	48.7%	42.5%	91.2%	8.8%	1.14	237	207	43	**487**
46	2	50.1%	41.1%	91.2%	8.8%	1.22	245	201	43	**489**
47	2	48.4%	43.3%	91.7%	8.3%	1.12	234	209	40	**483**
Sub-totals		49.1%	42.3%	91.4%	8.6%	1.2	716	617	126	**1459**
Totals Factorial One & Two		**47.3%**	**42.8%**	**90.1%**	**9.9%**	**1.1**	**1469**	**1330**	**308**	**3107**

Key : BLK = Orchard Block, **FACT** = Factorial, **male or fem.** = sex of plants male or female, **imm.** = immature
No.plnts = number of plants in each factorial by block.

Table V-2 : Factorial One - BiP coding system; and HortResearch accession code identification

Parents and ID's EXPT 1	PHS / MHS	DA02_03 (3-5-18e) 1	DA02_09 (3-5-16d) 2	DA03_03 (3-6-11d) 6	DA02_01_01_01 (41-4-9f) 7	DA01_03_20_03 (47-5-9b) 9	DA01_02_01_26 (Chieftain) 12	DA02_01_01_02 (41-3-9a) 13
DA01_03_18_01 (40-4-13f)	A	A01	A02	A06	A07	A09	A12	A13
DA01_03_20_01 (47-5-5d,Tomua)	B	B01	B02	B06	B07	B09	B12	B13
DA01_03_20_02 (47-5-10f)	C	C01	C02	C06	C07	C09	C12	C13
DA02_08 (3-6-20b)	D	D01	D02	D06	D07	D09	D12	D13
DA01_03_18_02 (40-1-16a)	E	E01	E02	E06	E07	E09	E12	E13
DA11_01 (36-4-0a,Beijing[25])	H	H01	H02	H06	H07	H09	H12	H13
DA01_02_01_05 (Bruno)	M	M01	M02	M06	M07	M09	M12	M13

Table V-3 : Factorial Two - BiP coding system; and HortResearch accession code identification

Parents and ID's / EXPT 2	*PHS* / MHS	*DA02_01_03_01 (40-6-10a)*	*DA01_02_01_19 (M52)*	*Riwaka C-2-115*	*DA01_03_20_04 (47-5-7d)*	*DA04_01 (3-2-19b,Paris#2)*	*DB01_04 (C6F5)*	*Riwaka A-6-28*
		3	**4**	**5**	**8**	**11**	**14**	**15**
DA03_02 (3-6-11b)	F	F03	F04	F05	F08	F11	F14	F15
DA06_01 (3-2-10b, 224)	I	I03	I04	I05	I08	I11	I14	I15
DA04_02 (3-2-11a, Paris #2)	J	J03	J04	J05	J08	J11	J14	J15
DA01_02_01_01 H18 (Jumbo)	K	K03	K04	K05	K08	K11	K14	K15
DA01_02_01_05 (Bruno)	M	M03	M04	M05	M08	M11	M14	M15
DB01_01 (C6M2) (3-2-11a, Paris #2)	N	N03	N04	N05	N08	N11	N14	N15

Table V-4: Factorial One - number of plants per plot (1-6), observed and measured for vegetative and fruiting characteristics in 1996.

♂		**Males**													
♀		**01**		**02**		**06**		**07**		**09**		**12**		**13**	
Female		**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**
	1	6		6	1	6		6		6	2	6	3	6	2
	2	6		6	!	6	1	6	1	6		6	2	6	2
A	**3**	6		6	1	6		6	1	6	1	6	2	6	
	4	6	2	6	1	6		6		6		6	1	6	1
	5	6	2	6	6	6	1	6		6		6	1	6	
	6	6		6	2	6		6		6		6	1	6	2
	1	6	1	6	2	6	4	6	2	6	2	**2**	1	6	2
	2	6	2	6	4	6	3	6	3	6	2	**3**		6	2
B	**3**	6	1	6		6	1	6	2	5	3	**1**		6	3
	4	6	1	6		6	1	5	1	6	1	**0**		6	1
	5	6	3	6	3	6	4	6	4	6	4	**1**		6	1
	6	6	2	6	3	6	3	6		6		**0**		6	2
	1	6	2	6	4	6	2	6	2	6	2	6	4	6	
	2	6	2	6	6	6	2	6	1	6	2	6	1	6	3
C	**3**	6	4	6	3	6		6	1	6	3	6	3	6	2
	4	6	1	6		6	1	6	2	6	1	6	3	6	2
	5	6	2	6	3	6	3	6	1	6	2	6	2	6	3
	6	6	4	6	2	6	2	6	1	6	3	6	1	6	2
	1	6	3	6	3	6				6	1	6	1	6	
	2	6	1	6		6	1			6	2	5	2	6	2
D	**3**	5	1	5		6		**1**		6	1	6	1	6	1
	4	6		6		6	2			6	1	6		5	
	5	6	2	6	2	6	1			6	1	6	1	6	3
	6	6	2	6	1	6				6		6		6	1
	1	6	1	**3**	2	6	1	6	1	6	3	6	1	6	2
	2	6	2	**3**	1	6		6		6		6	1	6	2
E	**3**	6	1	**3**	1	6	1	6	1	6		6	3	6	
	4	6		**2**		6	1	6		6		6	2	6	
	5	6		**2**		6		6	1	6	1	6	1	6	2
	6	6	2	**1**		6	1	6		6	1	6	3	6	
	1	6	2	5		6	1	5	1	6	1	5	1	6	1
	2	6		4	2	5	1	5	3	6	1	5	2	6	3
H	**3**	6	2	5	3	5	5	6	3	6	2	6	2	6	2
	4	6	1	5	2	6	3	6	2	6		6	2	6	1
	5	6	2	6	1	6	2	5		6	1	5		6	1
	6	6		4	1	5		5		5	1	3	1	6	2
	1	6	3	6	2	6	4	6	2	6	2	6	4	6	2
	2	5	3	6	2	6	3	6	3	6	1	6	4	6	3
M	**3**	6	2	6	3	6	1	6	2	6	4	6		6	4
	4	6	4	6	3	6	2	6	1	6	1	6	3	6	2
	5	6		6	3	6	3	6	3	6	4	6	2	6	
	6	6	3	6	1	6	3	6	2	6	1	6	4	6	

Key: VEG column = the number written is the number of plants per plot present and measured in 1996.
FRT column = the number written is the number of plants per plot present and measured in 1996,
NOTE an empty box indicates no data collected in 1996.

Table V-5 : Factorial Two - number of plants per plot (1-6), observed and measured for vegetative and fruiting characteristics in 1996.

♀ \ ♂		03		04		05		08		11		14		15	
	Plot	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**	**Veg**	**Frt**
	1	6	2	6	1	6	4	6	2	6	2	6	3	6	3
	2	6	1	5		6	3	6	1	5	1	6	1	6	1
F	**3**	6	5	6		6	2	6		5		6	1	6	2
	4	6	2	6	4	6	5	6	3	5		6		6	1
	5	6	2	6	2	6	2	6	2	5	1	5	2	5	3
	6	6	1	6		6	2	6	2	6	1	6	1	6	2
	1	6	3	6	2	6	6	6	1	6	2	6	2	6	5
	2	6	4	6	3	6	4	6	2	6	3	6	1	6	
I	**3**	6		6	2	6	4	6	3	6	1	6	2	5	1
	4	6	3	6	1	6	4	6	3	5	1	6		6	3
	5	6	4	6	1	6	6	6	5	6	2	6	1	6	3
	6	6	1	6		6	3	6	1	6	1	6	1	6	2
	1	6	4	6	1	6	5	6	2	6		6	2	6	2
	2	6	3	6	1	6	3	6	3	6		6	4	6	
J	**3**	6	2	6	3	6		6	1	6	1	6		6	1
	4	6	3	6	1	6	3	6	1	6	1	6	2	6	
	5	6	2	6		6	4	6	5	6	2	6	1	6	2
	6	6	1	6		6	3	6	1	6		6	1	5	2
	1	6	1	6	1	6	2	6		5	2	6		**3**	1
	2	6	2	6		6	2	6	1	6	1	6	1	**3**	1
K	**3**	5		6		6	2	6		6	2	6		**3**	
	4	6	1	6	1	6	2	6	2	5	2	6		**3**	
	5	6	1	6		6	3	6	1	5		6	1	**3**	
	6	6		6		6		6		6		6		**2**	
	1	6	1	6	2		3	6	1	5	2	6	3	6	2
	2	6	3	6	1	5	3	6		6	3	6	1	6	1
M	**3**	6	2	6	1	5	2	6		6	2	5	1	6	
	4	6	3	6	3		4	6	1	6	4	6	1	6	1
	5	6	1	6	3		3	6	2	6	4	6	3	5	3
	6	6	1	6	2		3	6	3	6	1	6	1	5	1
	1	6	2	6		6	3	6	2	6	1	6	2	6	2
	2	6	1	6	3	6	2	6	2	6	3	6		6	1
N	**3**	5	2	6	2	5	3	6	3	6	2	6	1	6	3
	4	6	3	6	3	6	3	6	4	6	2	4		6	2
	5	6	4	6	3	6	4	6	3	6	1	6		6	2
	6	6	2	6	3	6	2	6	2	6	1	6	2	6	3

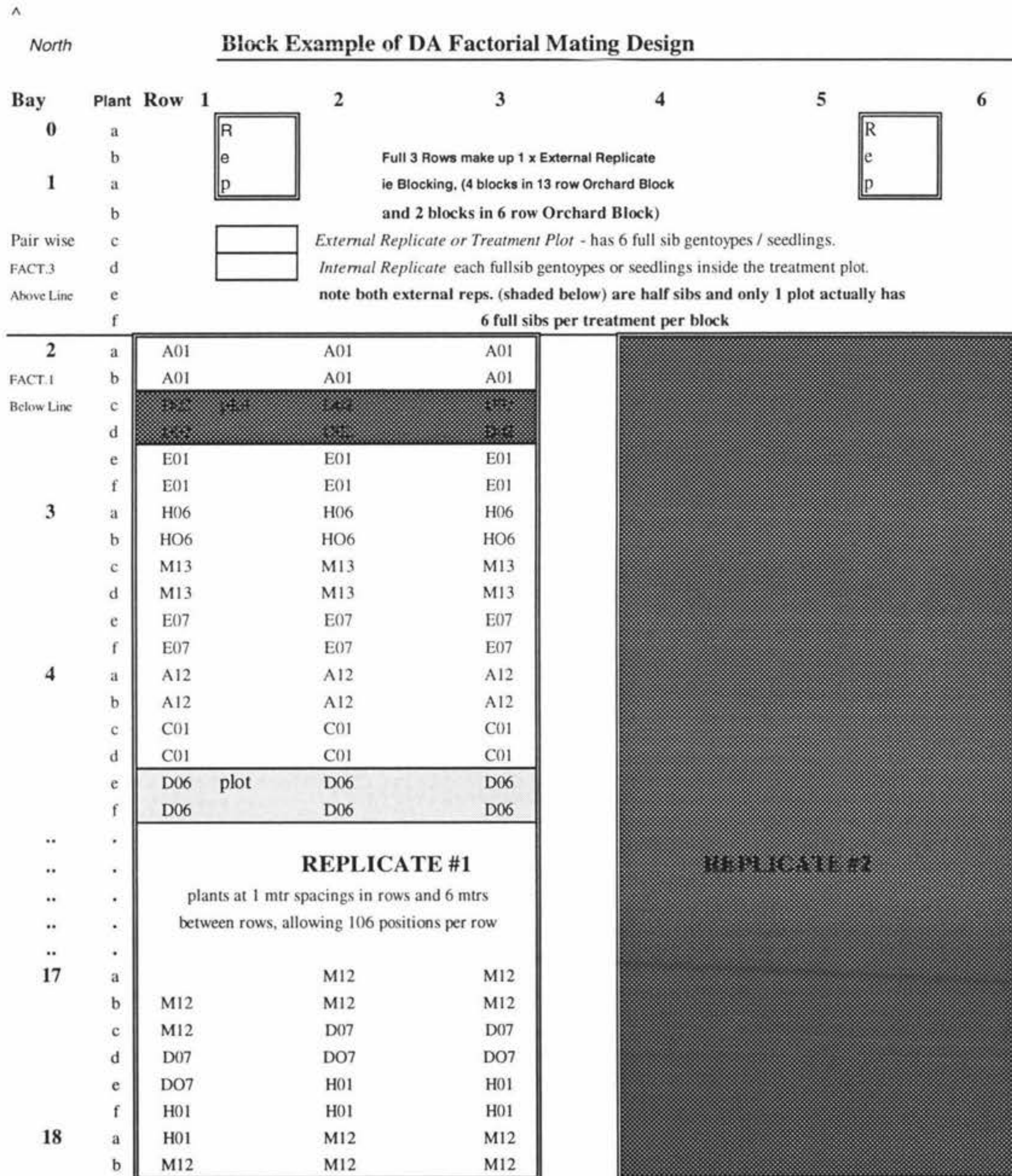
Key: VEG column = the number written is the number of plants per plot present and measured in 1996.
FRT column = the number written is the number of plants per plot present and measured in 1996,
NOTE an empty box indicates no data collected in 1996.

List of Abbreviations

A	Breeding value of an individual used as a parent
AAE or ($\propto$)	Average allele effect, (alpha or gene substitution)
ANOCOV	Analysis of covariance from procedure MANOVA in SAS®
ANOVA	Analysis of variance from procedure GLM in SAS®
BiP (s)	Bi-parental cross of parent A by parent B
factor A	Main factor A(effect) or female parental arrays GCA
factor B	Main factor B (effect) or male parental arrays GCA
factor A*B	First order interaction (effect) of female x male arrays SCA
F_1	Offspring of the first filial generation of a hybrid or population cross
FMD	Factorial mating design (based on NCMII)
GCA_{mean}	General combining ability means test
GCA_{var}	General combining ability variance test
HortResearch	The Horticulture and Food Research Institute of New Zealand Ltd
$\mathbf{h^2_a}$	Narrow sense heritability $\sigma^2_{G\ add.}/\ \sigma^2_P$ as defined by Falconer (1989)
$\mathbf{h^2_{dom}}$	Dominance heritability $\sigma^2_{G\ dom.}/\ \sigma^2_P$ as defined by Falconer (1989)
$\mathbf{h^2_{na}}$	Non-additive heritability $\sigma^2_{G\ na}/\ \sigma^2_P$ as defined by Falconer (1989)
IBP	Inference base population from the N.Z *A.deliciosa* 1991 germplasm
LSM	Least squares means
Kiwifruit	Generic term for fruit from *Actinidia deliciosa* var deliciosa
MANOVA	Multivariate analysis of variance from proc. GLM in SAS®
MCP	Mean sum of cross-products for ANOCOV
NCMII	North Carolina Model II design by Comstock and Robinson (1948)
NZKBP	New Zealand Kiwifruit Breeding Programme
NZKMB	New Zealand Kiwifruit Marketing Board
PDIFF	Probability of a difference between two LSM
POR	Parent off-spring regression
proc. GLM	Generalised Linear Model procedure for unbalanced data sets SAS®
r_a	Genetic correlation of two characters from a group of relatives
r_p	Phenotypic correlation of two characters from a group of relatives
RES	Relative efficiency of selection
SAS®	SAS® Institute Inc., Cary North Carolina.
SCA_{mean}	Specific combining ability with means test
SCA_{var}	Specific combining ability with variance test
SOV	Source of variation - classification of casual component
$t_{i's}$	Treatment effects in model

2. Appendix B: Experimental design and layout

Figure V-1 : General overview of the external replications layout of FMD design



each row has 2x2 plant positions +17x6 plant positions = 106

Figure V-2: General design format of the Factorial Mating Design in a randomised complete block. Orchard Blocks 35 & 40 - both have 12 rows (or 4 Blk'd replicates each). Orchard Blocks 46 & 47 - both have 6 rows (or 2 Blk'd replicates).

Overview of Factorial 1 (7x7) and Factorial 2 (6x7)

Orchard Block 35

Rows 1 2 3 4 5 6 7 8 9 10 11 12 13

Rows 1–3	Rows 4–6	Row 7	Rows 8–10	Rows 11–13
Bays Oa - 1f Guard Rows		Guard Row	Bays Oa - 1f Guard Rows	
Factorial 1 Rep 1 49 plots Bays 2a -18b	Factorial 1 Rep 2 49 plots Bays 2a -18b		Factorial 1 Rep 3 49 plots Bays 2a -18b	Factorial 1 Rep 4 49 plots Bays 2a -18b

Factorial 1 has 49 full sib families, = 49 plots/ rep.

Factorial 2 has 42 full sib families, = 42 plots/ rep.

each family is assigned to 1 plot per rep.

Guard rows occur at Northern most end of blocks, this is considered less optimal growing sites. Rows 7 in Blk35 and Blk 40 are also guard rows.

Orchard Block 40

Rows 1 2 3 4 5 6 7 8 9 10 11 12 13

Rows 1–3	Rows 4–6	Row 7	Rows 8–10	Rows 11–13
Bays Oa- 1f Guard Rows		Guard Row	Bays Oa- 4b Guard Rows	
Factorial 1 Rep 5 49 plots Bays 2a -18b	Factorial 1 Rep 6 49 plots Bays 2a -18b		Factorial 2 Rep 1 42 plots Bays 4c -18b	Factorial 2 Rep 2 42 plots Bays 4c -18b

Orchard Block 46

Rows 1 2 3 4 5 6

Rows 1–3	Rows 4–6
Bays Oa- 4b Guard Rows	
Factorial 2 Rep 3 49 plots Bays 4c -18b	Factorial 2 Rep 4 49 plots Bays 4c -18b

Orchard Block 47

Rows 1 2 3 4 5 6

Rows 1–3	Rows 4–6
Bays Oa- 4b Guard Rows	
Factorial 2 Rep 5 49 plots Bays 4c -18b	Factorial 2 Rep 6 49 plots Bays 4c -18b

Figure V-3: Pictorial view of the physical layout of each group of six plants/bay/row.

Bibliography

Allard R.W. (1960). *Principles of Plant Breeding.* New York: John Wiley & Sons, Inc.

Alston F.H. and P. Spielgel-Roy (1985). Fruit Tree Breeding: Strategies, Achievements and Constraints. In M.G. Cannell & J.E. Jackson (Eds.), *Attributes of Trees as Crop Plants.* (pp. 49-67). Great Britain: Natural Environment Research Council.

Beatson R.A. (1991). Genetic variation within a maternal half sib seedling population of *Actinidia deliciosa. Acta Horticulturae, No. 297,* 1,79-85.

Becker W.A. (1992). Manual of Quantitative Genetics. 191 pp. Academic Enterprises, Pullman, WA, U.S.A.

Beever D.J. and G. Hopkirk (1990). Fruit Development and Fruit Physiology. In I.J. Warrington & G.C. Weston (Eds.), *Kiwifruit Science and Management.* (pp. 97-126). Auckland: Ray Richards Publisher.

Bell R.L. and R.H. Zimmerman (1990). Combining Ability Analysis of Juvenile Period in Pears. *HortScience, 25,* 11,1425-1427.

Blanchet P. (1992). Breeding of kiwifruit and *Actinidia* at the Montauban School of Agriculture. *Arboriculture Fruitiere, No. 456, 46-51; 16 r.*

Blanchet P. (1995). New Variety of Early Kiwifruit, MontCap. *Arboriculture Fruitiere, No. 486,* 17-19.

Blanchet P. and J. Chartier. (1991). Genetic variability among the progeny of 'Hayward' kiwifruit. *Acta Horticulturae, No. 297,* 87-92.

Borojevic S. (1990). *Principles and Methods of Plant Breeding.* The Netherlands: Elsevier Science Publishing Company Inc.

Bringhurst R.S. (1983). Breeding Strategy. In J.N. Moore & J. Janick (Eds.), *Methods in Fruit Breeding.* (pp. 147-153).

Burdon R.D. (1986). Breeding long-lived perennials - frustrations, temptations, opportunities. *New Zealand Agronomy Society, Special Publication,* No.5,137-143.

Christie B.R. and V.I. Shattuck (1995). The Diallel Cross: Design, Analysis and Use for Plant Breeders. *Plant Breeding Reviews, 11,* 9-33.

Cockerham C.C. (1963). Estimation of Genetic Variances. In W.D. Hanson & H.F. Robinson (Eds.), *Statistical Genetics and Plant Breeding.* (pp. 53-94). Washington: National Academy of Sciences- National Research Council.

Comstock R.E. and H.F. Robinson (1948). Components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. *Biometrics, 4,* 254-266.

Comstock R.E. and H.F. Robinson (1952). Estimation of average dominance of genes in heterosis. In J.W. Gower (Ed.), *Heterosis.* (pp. 494-516). Ames: Iowa State College Press.

Cubero J.I. and J. Moreno-Gonzealez (1993). Selection Strategies and Choice of Breeding Methods. In M.D. Hayward, N.O. Bosemark, & Romagosa, I (Eds.), *Plant Breeding: Principles and prospects.* (pp. 281-313). London: Chapman & Hall.

Dekkers J.C. , L.K. Jairath and B.H. Lawrence (1994). Relationships between sire genetic evaluations for conformation and functional herd life of daughters. *Journal of Dairy Science, 77,* 3, 844-854.

Dickerson G.E (1969). Techniques for research in quantitative animal genetics. In: *Techniques and Procedures in Animal Science*, Albany, Nerw York

Dudley J.W. and R.H. Moll. (1969). Interpretation and Use of Estimates of Heritability and Genetic Variances in Plant Breeding. *Crop Science, 9,* 257-262.

Falconer D.S. (1989). *Introduction to Quantitative Genetics.* Essex, England: Longman, Harlow.

Ferguson A.R. (1990). The genus *Actinidia.* In I.J. Warrington & G.C. Weston (Eds.), *Kiwifruit Science and Management.* (pp. 15-35). Auckland: Ray Richards Publisher.

Ferguson A.R. and E.G. Bollard (1990). Domestication of kiwifruit. In I.J. Warrington & G.C. Weston (Eds.), *Kiwifruit Science and Management.* (pp. 165-246). Auckland: Ray Richards Publisher.

Ferguson A.R. , A.G. Seal , M.A. McNeilage , L.G. Fraser , C.F. Harvey and R.A. Beatson (1996). Kiwifruit. In J. Janick & J.N. Moore (Eds.), *Fruit Breeding, Volume II: Vine and Small Fruits Crops.* (pp. 401-417). John Wiley and Sons, Inc.

Fisher R.A. (1918). On the Correlation between Relatives on the Supposition of Mendelian Inheritance. *Transcripts of the Royal Society of Edinburgh, 52,* 399-433.

Gordon I.L. (1979). Standard errors of heritabilities based on perennial observations, with application to Yorkshire Fog grass. *Euphytica, 28,* 81-88.

Gordon I.L. , D.E. Byth and L.N. Balaam (1972). Variance of heritability ratios estimated from phenotypic variance components. *Biometrics, 28,* 401-415.

Graybill F.A. and W.H. Roberston (1957). Calculating Confidence Intervals for genetic heritability. *Poultry Science 36*, 261-265.

Graybill F.A. , F. Martin and G. Godfrey (1956). Confidence intervals for variance ratios specifying genetic heritability. *Biometrics, 12,* 99

Hallauer A.R. and J.B. Miranda (1981). *Quantitative Genetics in Maize Breeding.* Ames Iowa: Iowa S.U Press.

Hansche P.E. (1983). Response to Selection. In J.N. Moore & J. Janick (Eds.), *Methods in Fruit Breeding.* (pp. 154-171).

Hansche P.E. (1986). Heritability of Juvenility in Peach. *HortScience, 21,* 5,1197-1198.

Hansche P.E. and Beres, V (1965). An Analysis of Environmental Variability in Sweet Cherry. *Proceedings of the American Society for Horticultural Science, 88,* 167-172.

Hansche P.E. and V. Beres (1980). Genetic Remodelling of Fruit and Nut Trees to Facilitate Cultivar Improvement. *HortScience, 15,* 6,710

Hansche P.E. , V. Beres, V and Fordes H.I. (1972). Estimates of Quantitative Genetic Properties of Walnut and their Implications for Cultivar Improvement. *Journal of the American Society for Horticultural Science, 97,* 2, 279-285.

Hansche P.E. , Beres, V and R.M. Brooks (1965). Heritability and Genetic Correlation in Sweet Cherry. *Proceedings of the American Society for Horticultural Science, 88,* 173-183.

Hansche P.E. and R.M. Brooks (1965). Temporal and Spatial Repeatabilities of a Series of Quantitative Characters in Sweet Cherry (*Prunus avium* L.). *Proceedings of the American Society for Horticultural Science, 86,* 120-128.

Hansche P.E. , C.O. Hesse (1972a). Estimates of Genetic and Environmental effects on Several Traits in Peach. *Journal of the American Society for Horticultural Science, 97,* 1, 76-79.

Hansche P.E. , C.O. Hesse and V. Beres (1975). Inheritance of Fruit Size, Soluble Solids and Ripening Dates in *Prunus domestica* cv. Agen. *HortScience, 100,* 5, 522-524.

Hanson W.D. (1963). Heritability. In W.D. Hanson & H.F. Robinson (Eds.), *Statistical Genetics and Plant Breeding.* (pp. 125-138). Washington: National Academy of Sciences- National Research Council.

Harding J. , T. Byrne , H. Huang and Y. Yu (1991). Muilti Trait Selection in Flower Crops. In J. Harding, F. Singh, & J.N. Mol (Eds.), *Genetics and Breeding of Ornamental Species.* (pp. 157-178). Netherlands: Kluwer Academic Publishers.

Harvey C.F. , L.G. Fraser and J. Kent (1991). Actinidia seed development in interspecific crosses. *Acta Horticulturae, 1,* No. 297, 71-77.

Hayward M.D. , N.O. Bosemark and Romagosa, I (1993). *Plant Breeding Principles and Prospects.* Great Britain: Chapman & Hall.

Hayward M.D. and E.L. Breese (1993). Population Structure and Variability. In M.D. Hayward, N.O. Bosemark, & Romagosa, I (Eds.), *Plant Breeding: Principles and prospects.* (pp. 16-30). London: Chapman & Hall.

Henderson C.R. (1953). Estimation of Variance and Covariance Components. *Biometrics, 9,* 226-252.

Henderson C.R. (1969). Design and analysis of animal science experiments. *American Society of Animal Science, 1,*

HortResearch Kiwifruit Breeding (1996). 'Tomua' a New Early Kiwifruit Variety. *New Zealand Kiwifruit Journal, March.*

Hunt R. (1982). *Plant Growth Curves - The Functional Approach to Plant Growth Analysis.* London: Edward Arnold,

Janick J. and J.N. Moore (1983). *Methods in Fruit Breeding.* Purdue University Press., West Lafayette, Indiana.

Jensen E.L. and G.R. Barr (1971). Standard Errors of Heritability Estimates Calculated from Variance Component Analysis of a Two-way Classification. *Journal of Animal Science, 32,* 1069-1077.

Jinks J.L. (1981). The Genetical Framework of Plant Breeding. In H. Rees, R. Riley, E.L. Breese, & C.N. Law (Eds.), *The Manipulation of Genetic Systems in Plant Breeding.* (pp. 7-20). London: University Press, Cambridge.

Jinks J.L. and B.I. Hayman (1953). Analysis of diallel crosses. Maize Gen. *Co-operative Newsletter, 27,* 48-54.

Kearsey M.J. (1965). Biometrical analysis of a random mating population: a comparison of five experimental designs. *Heredity, 20,* 205-235.

Kearsey M.J. (1993). Biometrical Genetics in Breeding. In M.D. Hayward, N.O. Bosemark, & Romagosa, I (Eds.), *Plant Breeding: Principles and prospects.* (pp. 163-182). London: Chapman & Hall.

Kearsey M.J. and H.S. Pooni (1996). *The Genetical Analysis of Quantitative Traits.* London, UK: Chapman & Hall.

Kester D.E. ;P.E. Hansche ;Beres, V and R.N. Asay. (1977). Variance Components and Heritability of Nut and Kernel Traits in Almond. *Journal of the American Society for Horticultural Science, 102,* 264-266.

Kiwifruit Marketing Board (1997). Zespri. *New Zealand Kiwifruit Journal,*

Knight R.L. (1966). Progress in Breeding apples and Pears. *Proceedings Balsgard Fruit Breeding Symposium, 1,* 130-146.

Lamb J. (1995). Kiwifruit a Marketing Vision for the Year 2000. *The Orchardist, August,* 54-56.

Lavi U. , E. Lahal , C. Degani and S. Gazit (1992). The Genetics of Juvenile Phase in Avocado and its Application for Breeding. *Journal of the American Society for Horticultural Science, 117,* 6,981-984.

Lawes G.S. (1990). Propagation. In I.J. Warrington & G.C. Weston (Eds.), *Kiwifruit Science and Management.* (pp. 297-321). Auckland: Ray Richards Publisher.

Littell R.C. , R.J. Freund and P.C. Spector (1991). *SAS System for Linear Models.* Cary, North Carolina: SAS Institute Inc.,

Mather K. (1941). Variation and Selection of Polygenic Characters. *Journal of Genetics, 41,* 159-193.

Mayo O. (1980). *The Theory of Plant Breeding.* Oxford, England: Clarendon Press.

McDonald B. (1990). Precooling, Storage and Transport of Kiwifruit. In I.J. Warrington & G.C. Weston (Eds.), *Kiwifruit Science and Management.* (pp. 429-459). Auckland: Ray Richards Publisher.

McMath K.L. , V.J. Paterson and H. Young (1991). Factors affecting the sensory perception of sweetness and acidity in kiwifruit. *Acta Horticulturae, No. 297,* 1,489-500.

McNeilage M.A. (1991). Gender variation in *Actinidia deliciosa*, the kiwifruit. *Sexual Plant Reproduction, 4,* 267-273.

McNeilage M.A. (1997). Progress in breeding hermaphrodite kiwifruit cultivars and understanding the genetics of sex determination. *Acta Horticulturae*, No. 444,73-78.

McNeilage M.A. and J.A. Considine (1989). Chromosome studies in some *Actinidia* taxa and implications for breeding. *New Zealand Journal of Botany, 27,* 71-81.

Mettler L.E. and T.G. Gregg (1969). *Population Genetics and Evolution.* Englewood Cliffs, New Jersey: Prentice-Hall.

Moll R.H. and C.W. Struber (1974). Quantitative Genetics - Empirical Results Relevant to Plant Breeding. *Series of the North Carolina State University Agricultural Experiment Station, 26,*

New Zealand Fruit Council: Fruit Research in New Zealand 1994 and 1995. The Horticulture and Food Research Institute of New Zealand Ltd. (1995). Fruit Research 1994-5.

New Zealand Kiwifruit Journal (1997). New Zealand Kiwifruit Journal. *NZKMB*, January.

Nyquist W.E. (1991). Estimation of Heritability and Prediction of Selection Response in Plant Populations. *Critical Reviews in Plant Sciences, 10,* 3,235-322.

Osborne R. and W.S. Paterson (1952). On the sampling variance of heritability estimates derived from variance components. *Proceedings of the Royal Society of Edinburg, B64,* 456

Pringle G.J. , T.H. Marsh and R.G. Lowe (1991). Breeding for Early Maturity in Kiwifruit. *Acta Horticulturae*, No. 297, 99-108.

Sale P.R. and P.B. Lyford (1990). Cultural, Management and Harvesting Practices for Kiwifruit in New Zealand. In I.J. Warrington & G.C. Weston (Eds.), *Kiwifruit Science and Management.* (pp. 247-296). Auckland: Ray Richards Publisher.

SAS Institute (1989). *SAS/STAT Users Guide, Version 6.* Cary, North Carolina: SAS Institute Inc.

Saure M. (1987). Approaches and Achievements in Apple Breeding. In W.N. Chang & R.T. Opena (Eds.), *The Breeding of Horticultural Crops.* (pp. 81-90). Republic of China: FFTC Taiwan.

Searle S.R. (1958). Sampling variances of estimates of components of variance. *Annual Mathematics and Statistics, 29,* 167

Searle S.R. (1971). Topics in Variance Component Estimation. *Biometrics, 27,* 1-74.

Searle S.R. and C.R. Henderson (1961). Computing Procedures for Estimating Components of Variance in a Two-way classification, Mixed Model. *Biometrics, 17,* 607-616.

Simmonds N.W. (1979). *Principles of Crop Improvement.* London: Longman Group Limited.

Snedecor G.W. and W.G. Cochran (1967). *Statistical Methods.* Ames, Iowa, U.S.A: The Iowa State University Press.

Snowball A.M. , I.J. Warrington , L.A. Halligan and M.G. the late Mullins (1994). Phase change in Citurs: The effects of main stem node number, branch habit and paclobutrazol application on flowering in citrus seedlings. *Journal of Horticultural Science, 69,* 1, 149-160.

Steel J.H. and R.G. Torrie (1980). *Principles and Procedures of Statistics - A Biometrical Approach.* New York: McGraw-Hill Company.

Tancred S.J. , A.G. Zeppa , M. Cooper and J.K. Stringer (1995). Heritability and Patterns of Inheritance of the Ripening Date of Apples. *HortScience, 30,* 2,325-328.

Testolin R. , G. Cipriani and G. Costa (1995). Estimate of Variance Components and Heritability of Characters in Kiwifruit *(Actinidia.deliciosa). Acta Horticulturae, No. 403,* Part II:182-188.

Visser J. (1965). On the Inheritance of Juvenile period in Apple. *Euphytica, 14,* 125-134.

Visser J. (1976). A Comparison of Apple and Pear Seedlings with Reference to the Juvenile Period. II Mode of Inheritance. *Euphytica, 25,* 339-342.

Wang Z.M.(1995). Performance of the Kiwifruit variety 'Miliang 1' in Qianyang District. *Journal of Fruit Science, 12,* 268

Wei X.K. (1993). Xuxiang - a Promising Kiwifruit Variety. *China Fruits, No. 2,* 22-23.

Wricke G. and W.E. Weber (1986). *Quantitative Genetics and Selection in Plant Breeding.* Berlin: Walter de Gruyter,

Zhu D.Y.(1990). Phenotypic and genotypic variation in kiwifruit *Actinidia deliciosa* (A.Chev.) C.F Liang et A.R. Fergurson seedling populations. *Ph D thesis, Massey University, Palmerston North, New Zealand,* 175pp