This dissertation has been       65–13,012
microfilmed exactly as received

CORBEIL, Robert Roland, 1934–
  A GENETIC ANALYSIS OF MATURATION IN
  TOMATOES IN TERMS OF COMPONENTS OF
  EARLINESS.

University of Toronto, Ph.D., 1964
Biology—Genetics

University Microfilms, Inc., Ann Arbor, Michigan

A GENETIC ANALYSIS OF MATURATION IN TOMATOES
IN TERMS OF COMPONENTS OF EARLINESS


by

Robert R. Corbeil


A thesis submitted in conformity with
the requirements for the degree of
Doctor of Philosophy
at the
University of Toronto


1964

UNIVERSITY OF TORONTO

SCHOOL OF GRADUATE STUDIES


PROGRAMME OF THE FINAL ORAL EXAMINATION

FOR THE DEGREE OF DOCTOR OF PHILOSOPHY


OF


ROBERT ROLAND CORBEIL


11:00 a.m., Friday, May 15, 1964

School of Graduate Studies


A GENETIC ANALYSIS OF MATURATION IN TOMATOES

IN TERMS OF COMPONENTS OF EARLINESS


Committee in Charge:

Professor J. G. Breckenridge, Chairman
Professor K. C. Fisher
Professor L. Eutler
Professor G. M. Clark
Professor N. P. Badenhuizen
Professor D. B. DeLury
Professor T. E. Reed
Professor P. Sarkar
Professor I. Tallan
Professor R. Wormleighton

THESIS

# A GENETIC ANALYSIS OF MATURATION IN TOMATOES

## IN TERMS OF COMPONENTS OF EARLINESS

The genetic mechanisms of maturity in Lycopersicon were examined with reference to its major components; seeding to first bloom, first bloom to fruit set, and fruit set to ripe fruit; in three experimental designs. The first approach utilized gene markers, especially those of chromosome two, to locate effects of earliness in the tomato genome. The second method employed seven varieties selected for their range of values in the expression of maturity, plus the 21 possible hybrids, and analyzed by constant parent regression techniques. The final method involved two varieties, their $F_1$, $F_2$, and $F_3$ generations and partitioned total phentypic expression into additive, dominance, epistatic, and environmental effects.

It was determined that the major genes for maturity were located on the number two chromosome with at least two distinctly separate regions. One region, associated with the mottled and dwarf gene markers, was approximately twice as influential as the other which was closely associated with the marker compound inflorescence. All three components showed similar results. Each component, however, contributed unequally to total maturity i.e. as measured in days from seeding to ripe fruit. A non-additive effect was found between the two defined regions of chromosome two in the components first bloom and fruit set.

All analyses were completed on the original scale as measured in days. Scaling tests indicated that a transformation of the data could simplify the analyses, but a satisfactory scale could not be found in which all loci would become additive. Care had to be given, therefore, to extract interaction effects.

It was found that early maturity genes were completely dominant to their late phase alleles in the components ripe fruit and fruit set, and partially dominant in the component first bloom. The interaction or epistatic effects in segregating generations were of the same magnitude as those of additivity. For the component first bloom the two regions of chromsome two which had effects on maturity could be regarded as being equivalent to two genes, one having twice the value of the other. With the added information provided from partitioning methods a hypothetical $F_2$ distribution was calculated which included epistatic effects. The hypothetical and actual $F_2$ distributions were in very good agreement.

In the component ripe fruit the two regions of chromosome two which in luence maturity could not be equated to two loci

as in the component first bloom. At least 5 independent gene pairs were detected statistically. A hypothetical $F_2$ distribution was calculated in the same fashion as that calculated for the component first bloom. The agreement between the hypothetical and the actual distributions was not clear. The total $F_2$ distribution consisted of four replications and independent tests were made on each. The results were inconsistent due to heterogeneity. Nevertheless, the premises upon which the hypothetical distribution was based were concluded as the most reasonable under the conditions of the experiment.

The analysis of the component fruit set was not as thorough because of the shortcomings associated with it. Measurement of this component in whole days was found to be too crude to justify extensive analysis.

It was concluded that because a scale which would render all loci additive could not be found, the most important single aspect to come from these analyses was that of evaluating interaction (epistasis). In the component first bloom two types of epistasis were detected. A homozygous locus interacting with a heterozygous locus with a heterozygouslocus interaction by another approach. In the component ripe fruit, only a heterozygous-heterozygous type interaction could be positively identified, whereas in the component fruit set the interactions were similar to those of first bloom. As the environment was not constant through all components it played a significant role in diversifying genetic behavior.

## BIOGRAPHY

| | |
|---|---|
| 1934 - | Born, Biddeford, Maine, U.S.A. |
| 1958 - | B.S. Ed. Gorham State Teachers' College, |
| 1961 - | M.S. University of Maine |
| 1963 - 1964 | National Research Council Studentship |
| 1961 - 1964 | School of Graduate Studies, University of Toronto |

## GRADUATE STUDIES

Major Subject:

Genetics                    Professor L. Butler

Minor Subjects:

Radiation Biology          Professor G. M. Clark

Statistics for Engineers   Professor R. Wormleighton

## ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Dr. K. C. Fisher and members of the Department of Zoology, University of Toronto, who have been a source of encouragement in the course of graduate studies; especially to Dr. L. Butler for his guidance as thesis advisor, for providing the stock material, and for assistance with the expense of carrying on the research; and to Drs. T. E. Reed and I. Tallan for reviewing the manuscript.

The author is also indebted to Drs. G. C. Ashton, Department of Physics and Mathematics, J. C. Rennie, Department of Animal Husbandry, Ontario Agricultural College, for making electronic computer facilities available; and to Dr. R. J. Hilton, Head, Department of Horticulture, for providing greenhouse and field space.

Acknowledgement is due to the National Research Council of Canada for financial assistance granted through a studentship.

ii

# TABLE OF CONTENTS

iii

# LIST OF TABLES

iv

LIST OF FIGURES

# INTRODUCTION

## 1. General

At the time the work of Mendel was rediscovered there were already active genetical research "cliques" pursuing investigations and advancing their own theories. Although they contributed little to genetical theory as we have it today they had, nevertheless, importance of their own. These were mostly the efforts of biometricians. W. Johannsen (1903) discussed the most prominent theories of this day, with their new possibilities, in the light of his own work with pure lines. He wrote of deVries' "Mutationstheorie" of 1889 and Galton's "Stirp" theory which had already been worked out in 1876.

The persisting line of quantitative genetical research can be said to have been initiated by Francis Galton in 1889 with the publication Natural Inheritance. This was continued by Karl Pearson with added impetus given by Nilsson-Ehle and East. It was Sir Ronald Fisher in 1918, however, who formulated the basic concepts still firmly held today. Oscar Kempthorne (1957) in the preface of a most comprehensive text of quantitative genetics, An Introduction to Genetic Statistics, confesses that essentially all the statistical methodology given in his book traces back to Fisher's work, and especially the theory of quantitative inheritance presented traces back to a single paper of his (Fisher, 1918).

Since the onset of modern biometrical genetics other workers who made lasting impressions and can still draw direct lineage from

- 1 -

Galton's original work are found among the advocates of Sewall Wright and J. B. S. Haldane. In recent years J. L. Lush has been the primary proponent in keeping Wright's early work from being buried in the recent literature.

The diversity of present day statistical models appear for the most part to have strong developmental relationship to Fisher's early work, and as expected the similarities are often fundamental. The main part of the work embodied in this dissertation depends on a very particular lineage of geneticists, based primarily on Fisher, Immer, and Tedin's (1932) model, dwelling mostly on Mather's (1949) work, and with some introduction of Hayman's more recent developments (1958; and Mather, 1955).

2. Statistical models

Mather (1949) introduced practical tests and methodology for extracting from experimental data certain genetic parameters. With the long accepted notion that continuously variable traits were controlled by a number of discrete Mendelian units he developed a model of second degree statistics, more widely known as the partitioning of variation. Each partition becomes the estimate of a genetic parameter as had been introduced by Fisher (1918) and Fisher, Immer, and Tedin (1932).

To describe the genetic variation present in two inbred lines and their descendant families, under the assumption of no epistasis, Mather showed that the variance of each generation contained three components. First, the variation that is independent of the genetic system insofar as it is non-heritable and arises from environmental

agencies. This he denoted by E. The second component arises from the average difference between the two true breeding parents and may be ascribed as fixable variation. Mather denoted fixable variation as the component D. Finally, the third component is due to the variation created by intra-allelic interaction and is named unfixable or H.

Falconer (1961) described the same components as additive A, instead of D; dominance D, rather than H; and used E in similar fashion. By introducing the component I, for interaction as expressed by epistasis Falconer eliminated the assumption which is necessary in Mather's model. As the parameter I must have a complex nature, and Falconer is far from clear on how this component can be extracted in its presented form, it will be overlooked for the time being.

To examine the meaning of D and H in genetical terms we equate them to Fisher, Immer, and Tedin's (1932) terms and derive the useful form by Mendelian theory.

$$D = \Sigma(d^2)$$

$$H = \Sigma(h^2)$$

where $\overset{+}{\underset{-}{d}}$ is the measured increment ascribably to a homozygotic locus from the midparent value, and $\Sigma(d^2)$ is the sum of all such increments squared over all loci. Likewise, h, is the increment of the heterozygote from the midparent and $\Sigma(h^2)$, the sum of all such increments squared (see Fig. 1 for a one locus representation).

$$AA \underset{+d}{\overset{Aa \xrightarrow{\quad h \quad} M.P.}{\rule{8cm}{0.4pt}}} \underset{-d}{\quad} aa$$

Fig. 1

The most restrictive assumption in the model of course is

that of no epistasis where epistasis in some form or other is so often
manifested in actuality. As Mather (1949) points out, however, it
need not be of concern if a satisfactory transformation of the data
is found.

Interaction was earlier considered by Fisher (1918), and
Rasmusson (1933). Mather (1949) introduced tests for detecting
epistasis using generation means. These were elaborated upon by
Cavalli (1952), Anderson and Kempthorne (1954), Hayman (1957) and
others. Models elaborating certain epistatic systems were described
by Griffing (1950), Powers (1950), and Horner, Comstock and Robinson
(1955). More general models were developed by Anderson and Kempthorne
(1954), Hayman and Mather (1955), and Hayman (1958). All these
tests were mostly with generation means. Cockerham (1957) expressed
doubtful concern with the efficacy of using generation means. Only
one of the foregoing papers (Hayman and Mather, 1955) involved epistasis
in terms of second degree statistics and they theoretically demonstrated
how epistasis effected the main components.

Mather's (1949) tests of additivity are based on the fact
that each genotype progresses independently from any other genotype
through the descendant families. Thus D and H are always $\Sigma(d^2)$ and
$\Sigma(h^2)$ through the generations without interaction terms. To test
the additivity of the $F_2$ generation, Mather (1949) stated by formulae
that for each locus the $F_2$ value should equal $1/2 \, F_1 + 1/4 \, P_1 + 1/4 \, P_2$,
where $P_1$ represents one parent and $P_2$ represents the other parent.
For a number of loci which are additive, that is, independent of interloci
modifications of any sort, the mean of the $F_2$ should be equivalent to

$1/2\ \bar{F}_1 + 1/4\ \bar{P}_1 + 1/4\ \bar{P}_2$ or $4\ \bar{F}_2 - 2\ \bar{F}_1 - \bar{P}_1 - \bar{P}_2 = 0$, with variance $16\ V_{\overline{F2}} + 4\ V_{\overline{F1}} + V_{\overline{P1}} + V_{\overline{P2}}$ . Obviously with epistasis the variance of the expression is underestimated, nor does the linear model approach zero. Anderson and Kempthorne (1954) pointed out, however, that Mather's model for testing additiveness as presented above is effective only for the highest order interaction. For example, in a trigenic system, Mather's model may not detect epistasis and the conclusion of additivity is legitimate only in reference to the triple interaction A x B x C and does not necessarily hold for interactions A x B, A x C, and B x C. Some precautions can be taken to partly safeguard against this. Hayman and Mather (1955) demonstrated that by using backcross as well as $F_2$ and $F_3$ generations a type of interaction not detected in one generation may be detected in another because all generations are not equally sensitive to all forms of epistasis. Where in a digenic system heterozygote x heterozygote interaction occurs it is most likely to effect the $F_2$ test for additivity, whereas comparing the backcrosses reflects a homozygote x heterozygote interaction more easily. This is still no perfect guard against failing to detect digenic interactions when a higher number of loci are influencing the trait but, it should make detection more probable. In addition Hayman (1958) demonstrated that statistically significant interactions higher than digenic ones occur infrequently.

It is concluded by many that the ideal model for identifying the nature of the epistasis as well as extracting main effects would be one in which all genotypes could be identified, but this is not the easiest thing to do. A method that would allow accurate estimates

of the number of effective factors (gene pairs) would go a long way in furthering quantitative inheritance in a practical sense. Some success has been demonstrated by Currence (1938), Powers (1939a, 1939b) in tomatoes, Breese and Mather (1957, 1960), and Gilbert (1960) in Drosophila. These investigators followed the segregation of a quantitative trait in terms of Mendelian markers. This enabled them to allocate with varying degrees of precision areas of chromosomes influencing the character under study. For its many advantages it has in general a nearly insurmountable difficulty. Not all the material one would wish to investigate quantitatively is well defined in terms of Mendelian genetics.

Powers, Locke, and Garrett (1950) succeeded by some seemingly intuitive method of separating 27 genotypes into 18 classes resulting from the segregation of four genes in two backcrosses and an $F_2$ generation. The character under investigation was the percentage of flowers which set fruit in a cross between two varieties of Lycopersicon esculentum.

Working with rice Mohamed and Hanna (1964) compared Mather's (1949) and Powers', et. al. (1950), Leonard, Mann, and Powers (1957) methods of partioning and concluded that under the conditions of their experiment the parameters obtained by Mather's partitioning method were unreliable. However, they did not report tests for linkage or epistasis and these would have been interesting since there were clear departures in the observed estimates of the mean variance of $F_3$ families and that expected. As Mather (1949) pointed out, with linkage the parameters estimated by D and H would remain homogeneous

through $V_{F2}$, $V_{\overline{F3}}$, $W_{F2/F3}$ and differ in the $\overline{V}_{F3}$ only. This may not prove to be significant in Mohamed and Hanna's (1964) work but, it appears somewhat suspicious. They favored a two factor model and though this may be quite satisfactory on a practical basis the data in Leonard, Mann and Powers' model as well as in Mather's suggests a higher number of effective factors.

Another model of interest developed in recent years has been one using only inbred lines and $F_1$ hybrids of all possible matings. Griffing (1948, 1950) is primarily responsible for the development of constant parent regression techniques, and the elaboration of diallel cross analysis is the work of Hayman (1954, 1957). These methods do not rely on segregating generations and, therefore, provide economy of number and simplicity of interpretation. However, they are limited to the analysis of gene action and interaction and do not allow partitioning of additive and dominance from genetic variation. The diallel cross method appears to yield slightly more information but it necessarily contains reciprocal crosses, whereas, constant parent regression methods do not.

Griffing (1948, 1950, 1953) and Burdick (1949, 1954) have applied the method of constant parent regression and have shown its simplicity and practicality for determing gene action. To be reliable these techniques depend largely on the selection of a wide range of parents representing as many different genotypes as possible. This introduces a variety of backgrounds in the parents which may interact to prevent a clear analysis. As Kempthorne pointed out (1955) it does not seem reasonable to assume that only two allelic forms of

the gene occur at any one locus except in the case where the analysis
is of two inbred parents and their descendant families. Nevertheless,
these shortcomings are overcome in part by proper selection of materials.
Furthermore, in practice the model has helped investigators to make
quite reasonable assessments of the system under study.

In the models reviewed the variances of univariate data only
were partitioned to extract estimates of the genetical parameters.
For the most part these models can be extended to partition the
covariance of paired measurements or of measurements of two or more
characters. Cockerham (1954, 1956, 1957) developed a model utilizing
a factorial design and orthogonal comparisons for partitioning the
variance and covariance but again some knowledge of genotypic
frequencies was required. By first obtaining an estimate of
heritability, defined as the ratio of genetic variability to total
variability, Clayton, Knight, Morris, and A. Robertson (1957) and
F. W. Robertson (1957a, 1957b) partitioned the variance and covariance
of several of the quantitative characters in Drosophila. Lerner (1950)
and A. Robertson (1955, 1959) outlined various methods of extracting
heritability estimates from data.

## 3. Estimating environmental error

Up to now we have been primarily concerned with the partitioning
of genetic variation but, before this can be done, the genetic
variance must first be extracted from the total or phenotypic
variation. The oldest and still most common method used, probably
because of its ease of application, involves subtracting the combined
variance of true breeding parent lines from lines which are either mixed

or segregating. The inbred lines are considered homozygous and are variable for reasons other than genetical, hence serve as the estimate E, environmental error (Falconer, 1961; Clayton, Knight, Morris, and A. Robertson, 1957; F. W. Robertson, 1957b; and others). Powers (1942) on the other hand drew a regression line of means on variances using non-segregating generations. He extracted segregating generation variances by estimating the environmental variance from the generation's mean on the regression line and subtracting it from the observed variance. Panse (1940) criticized these methods on the ground that they assumed all genotypes interacted with the environment in similar fashion. To overcome this difficulty the generalized error term of an analysis of variance is extracted from all generations (Cockerham, 1954, 1957; Hayman, 1954, 1957; Kempthorne, 1957; and others). In Mather's (1949) model a least squares method combining all generations including $W_{F2/F3}$, which has no error term is also valuable. A similar hypothesis is the method of weighted least squares as used by Cavalli (1951) which has great value in experiments in quantitative inheritance for extracting a number of parameters from a series of generations. The value lies in the weights giving greater influence to generations with larger number of observations and thus rendering greater precision to the estimates of the parameters.

4. <u>Quantitative inheritance in tomatoes</u>

Rick and Butler (1956) reviewed the field of quantitative inheritance in tomatoes thoroughly. Few papers of a quantitative nature have appeared in the literature since. Hayman (1958) reviewed some of Powers' (1951) results on number of locules. Powers (1963)

elaborated on the partitioning method presented in 1950 (Powers, Locke, and Garrett, 1950). Kheiralla and Whittington (1962) presented a new approach in tomato genetics. Using Hayman's (1954) work of the analysis in diallel experiments, they studied the inheritance of total dry weight, leaf area, fruit yield, and net assimilation rates. The authors felt that the paper's main contribution to originality was the evaluation of factors in time. At least one other work is in preparation but is not in the literature.

Although there are five or six types of models of quantitative inheritance in the literature, research in the tomato until Kheiralla and Whittington (1962) was limited to Powers, Locke, and Garrett's (1950) model and Griffing's (1950) constant parent regression techniques. However, a considerable amount of work has been done on the behavior of continuously variable traits with little or no emphasis of the genetical mechanisms underlying their behavior (Groth, 1915; Wellington, 1922; Butler, 1941; MacArthur, 1941; and others). Particularly in fruit size interest abounded in the peculiar behavior of the $F_1$ in relation to its parents (Groth, 1914; MacArthur and Butler, 1938; Butler, 1941).

Currence (1932, 1938) and Yeager (1937) made efforts to combine quantitative with qualitative genetics and thus present some of the first gene behavior analysis in tomatoes. Currence (1938) concerned himself with earliness and showed that the number two chromosome clearly had all the major factors influencing earliness. Yeager (1937) reported the correlations which existed in fruit size with fruit shape gene mutants.

The most popular quantitative character studied in tomatoes

has been fruit size. Considering fruit size as a component of yield
and other components as locule number, percentage of flowers to set,
number of fruits, weights, number of flowers per truss, and combination
of these characters would account for at least some two dozen papers
(Powers, 1950; Powers and Lyon, 1941; Myers, 1924; and others).
Earliness of course is not altogether independent of yield either
and was included in some cases.

The components of maturity are somewhat less popular,
Powers, Locke, and Garrett (1950), and Burdick (1954) produced the
main efforts along these lines. Powers, et. al. (1950) divided maturity
into three stages; 1) seeding to first bloom; 2) time from first
bloom to first fruit set; and 3) from fruit set to first ripe fruit.
He concluded from his studies that at least three gene pairs
differentiated parents in the first and second stages combined and
two in the third stage. He thought that at least some gene pairs were
common to all stages, and reported eight gene pairs differentiated
the parents for the three stages combined. Burdick (1954) by constant
parent regression techniques found a high incidence of heterosis in
all stages of development and in combination of stages. Where the
studies can be compared (Currence, 1938; Griffing, 1948; and 1954;
Powers, Locke, and Garrett, 1950; and Burdick, 1954) only minor
discrepancies can be found among the results.

Such other characters as ovary size (MacArthur, unpubl.;
Butler, unpubl.), seed size (Snyder and Larson, 1955), total dry
weight, and assimilation time (Kheiralla and Whittington, 1962) have
also been investigated.

## 5. Objectives

Statistical theory is ahead of application in the field of quantitative inheritance and the form of existing methodology cannot be easily followed by the non-initiated. Foremost on the list of objectives then would be one of familiarization.

From there the purposes of this work are centered on application of various models using a range of methods. Parameters are evaluated and where it is possible generalizations are drawn. The scope of the work is, therefore, to be necessarily broad, designed in favor of certain models but not exclusively so. It surveys the literature predominantly concerned with quantitative inheritance as is distinguished from general population genetics. Causal analyses and most of Sewall Wright's contributions to the general field are not seriously considered as their applications have a different basis.

Finally, it is hoped that a conclusive analysis of the inheritance of maturity can be achieved.

MATERIALS AND METHODS

There were three experiments basic to this work, combined to produce a comprehensive analysis of the genetic mechanisms underlying the inheritance of maturity and its components. All three experiments made use of selected varieties of tomatoes. The varieties (table 1) were selected for their differences in the expression of earliness and limited to those which were known to be successful in the southern Ontario climate.

Table 1. Time in days from seeding to ripe fruit for varieties and lines of tomatoes used in the three experiments.

| VARIETY | | MEAN $\pm$ S.E. | LINE | | MEAN $\pm$ S.E. |
|---|---|---|---|---|---|
| Red Currant | | 92.6 $\pm$ 0.83 | 49:75 | | 126.0 $\pm$ 1.43 |
| Yellow Cherry | | 95.7 $\pm$ 0.68 | | | |
| Fireball | | 108.5 $\pm$ 0.97 | T2006 | | 126.1 $\pm$ 1.64 |
| U.S.D.A. | | 113.6 $\pm$ 1.50 | | | |
| John Baer | | 113.9 $\pm$ 1.05 | 3213 | | 127.7 $\pm$ 1.23 |
| Rutgers | | 123.4 $\pm$ 1.23 | | | |
| Tangerine | | 123.6 $\pm$ 1.00 | T2003 | | 133.7 $\pm$ 1.66 |

1. First experiment

In the first experiment all varieties and lines used were of the species _Lycopersicon esculentum_. The lines were selected for their genetic markers and their lateness of maturity whereas the varieties were selected for earliness. All were procured from Dr. L. Butler of the Department of Zoology, University of Toronto and the lines were denoted by him as: T2003, T2006, 49:75, and 3213. The

- 13 -

markers contained therein were from each of the major chromosomes of the tomato genome and especially of chromosome number two which had been shown by Currence (1932, 1938) to contain the major effects of earliness. These lines were crossed with the varieties Yellow Cherry and Fireball selected for their earliness.

The parent plants were grown and maintained for crossing in the greenhouses of the Department of Horticulture at the Ontario Agricultural College. The desired crosses were made during the fall and winter of 1962-63 in preparation for the summer of 1963. $F_1$ seed was produced by crossing all four late lines ($\male\male$) to each of the two early varieties ($\female\female$). The four late lines ($\male\male$) were further crossed to the $F_1$'s ($\female\female$) to produce the backcross seed to be planted that summer.

The design was to plant parents, $F_1$'s, and backcross material in one experiment to enable comparisons and checks on the segregation of genetic markers with earliness. Each block of the experiment was represented by one plot of each of the 6 parents and the 8 $F_1$'s, two plots of each of the 4 backcrosses involving the lines 49:75 and 3213, four plots of the backcrosses involving T2006, and nine plots of the backcrosses with T2003. Each plot contained 10 plants and the experiment had 3 blocks. A greater number of backcross plots of T2003 and T2006 was necessary because of the linkage of most of the markers, whereas, there existed little or no linkage of the markers in the lines 49:75 and 3213. The number of plants used of T2003 and T2006 backcrosses was limited only by the success with which the seed was produced and germinated. The markers of each of the lines are given and briefly

explained in table 2.

      The analysis proceeded in a classical manner.  The plants were segregated into phenotypic classes and their values in days for each of the components of maturity calculated.  Comparisons were made between phenotypic classes to evaluate given chromosomes, or portions thereof, in their influence on earliness.

Table 2.    Description of lines T2003, T2006, 49:75, and 3213 and the marker genes used in each.

| MARKER | NO. OF CHROMOSOME WHERE LOCATED | DESCRIPTION* |
|---|---|---|
| **LINE T2003** | | |
| m | 2 | mottled leaf |
| d | 2 | dwarf plant |
| p | 2 | peach fruit |
| aw | 2 | green stem |
| o | 2 | ovate fruit |
| sp | 6 | self pruning plant |
| | | |
| **LINE T2006** | | |
| m | 2 | mottled leaf |
| d | 2 | dwarf plant |
| p | 2 | peach fruit |
| o | 2 | ovate fruit |
| s | 2 | compound inflorescence |
| r | 3 | yellow flesh |
| | | |
| **LINE 49:75** | | |
| br | 1 | brachytic plant |
| y | 1 | colorless epidermis |
| wf | 3 | white flower |
| c | 6 | potato leaf |
| gs | 7 | green striped fruit |
| | | |
| **LINE 3213** | | |
| f | 11 | fasciated fruit |
| j | 11 | jointless pedicel |
| wt | 5 | wilty leaf |
| H | 10 | hairy stem |
| al | 8 | anthocyanin loser |
| d | 2 | dwarf plant |

\* For a complete description see Rick and Butler (1956)
Chromosome two linkage in map units  m 2 d 4 p 10 aw 2 o 34 s
and other linkages  br 30 y ; and f 65 j.

## 2. Second experiment

The second experiment was designed mostly in favor of studying gene action as did Griffing (1950) by constant parent regression techniques. For this purpose a wide range of parent varieties was selected from the species L. esculentum and L. pimpinellifolium. There were six varieties of the first species, namely: Yellow Cherry, Fireball, U.S.D.A. #223311, John Baer, Rutgers, MacArthur's Tangerine; and one of the latter species, Red Currant, because of its extreme earliness. The lateness of some of the varieties chosen had to be compromised to the length of the expected growing season. The overall maturity time in days was shortest for Red Currant and Yellow Cherry and the longest for Rutgers and Tangerine (table 1). Because of the cross section of genotypes represented in this experiment as inbred lines, certain relationships were established with the other two experiments. It was anticipated that from these relationships valid generalizations could be drawn which otherwise would have been impossible from the combined experiments. Crosses were made of all possible pairs of parents, randomly selecting the female parent for each pair. This produced 21 $F_1$ hybrid varieties. The 28 parents and hybrids were grown during the summer of 1963 in a block comprising one plot of the varieties with three plants in each plot and four blocks to the experiment. The experiment was analyzed for each component by an analysis of variance for randomized complete block design with subplots and the means of the 28 varieties were further analyzed by constant parent regression techniques as developed by Griffing (1950) and modified by Burdick (1954).

## 3. Third experiment

Using the earliest and latest of the varieties available for this climate the inter-specific cross of Red Currant (<u>L</u>. <u>pimpinellifolium</u>) and MacArthur's Tangerine (<u>L</u>. <u>esculentum</u> <u>var</u>.) with its $F_1$, $F_2$, and $F_3$ generations were grown. This was the bulkiest of the experiments and required two winters and two summers to complete. During the fall and winter of 1961-62 preparations were made to plant parents, $F_1$, $F_2$ and two backcross generations of this cross Red Currant (♂) with Tangerine (♀). Initially the efforts were to have reciprocal crosses represented, but a high incidence of disease in the seedlings in the spring of 1962 raised much havoc with the experiment as planned. Flats of seedlings showing disease were discarded immediately and better than 60% of the material was lost. Only a few parents remained and a fair number of $F_1$'s $B_E$ (backcross to early parent), and $B_L$ (backcross to late parent). None of the $F_2$'s were lost. From these, 60 plants were randomly selected and selfed to give rise to the 60 $F_3$ families used in the 1963 experiment. A very limited use of the remaining plants from the 1962 experiment was made and then only as preliminary information. Due to limited field space and the time required daily to examine a large number of plants the 1962 experiment could not be repeated. Its intended purpose, which was to mimic Powers', et. al. (1950) work and compare it to other models grown concomittantly was abandoned.

During the spring of 1963 plants of the parents, Red Currant and Tangerine, the $F_1$, $F_2$, and 60 $F_3$ families were transplanted to the field in an experiment consisting of four blocks, each with 100 randomly

arranged plots. Of these plots 8 were of Red Currant, the early

parent; 8 of Tangerine, the late parent; 4 of the $F_1$, 20 of the $F_2$,

and one each of 60 $F_3$ families. Each plot consisted of seven plants.

The blocks were analyzed individually for the variances of the $F_2$ and

mean of $F_3$ families, the mean variance of $F_3$ families, and the

covariance of the mean of each of the $F_3$ families with its parent $F_2$

plant. This entailed estimating the variance of each of the 400 plots

for each of the components as well as the covariance of the $F_3$ means

with their $F_2$ parent. Further, the covariances of all pairs of

measured components were calculated for purpose of examining their

correlations. The blocks were then reassembled for an analysis of

the variances and covariances estimated for each generation. The

parent and $F_1$ plots were used to estimate directly the environmental

errors within and between plots. However, the final estimates of D,

H, $E_1$, and $E_2$ were extracted by combining all data in a least squares

method (see Mather, 1949).

4. **Miscellaneous techniques**

Seed collecting, storage, and planting techniques were those

common to long existing horticultural practices. The desired fruits

were collected and their seeds spread on a sheet of paper to dry.

The seeds were not cleansed in order to allow them to stick to the

sheet on which was recorded their phenological and genetic identification.

At planting time the seed was picked from these sheets and placed into

labelled envelopes. Approximately 200 seeds were planted per flat of

soil which had been prepared with ten rows grooved into the soil of

the flat. Each row was identified by labels with the seed's identification,

all information had been coded for ease and convenience of handling.
The seed planting was completed in one day in the greenhouses four
weeks prior to field time. On the third and fourth day after germination
each seedling was transplanted into an individual peat pot. The
plants were then left undisturbed except for feeding and watering until
they were put into the fields, pots included. Approximately 6,000
plants were transplanted to the field, some, however, were used as
guards along each side of the fields and for separating experimental
blocks. Somewhat more than 4,000 plants were examined daily.

5. The components of maturity

     The plant was termed mature as soon as a fruit on it
showed colors of ripening. Conceptually, there were many other ways
of defining maturity, this was deemed the most practical and the
simplest for our purpose. The process of maturation begins with the
planted seed and is fully expressed with the first ripe fruit. This
process then had components which could conveniently be identified and
by which the parents contrasted in measurement. These stages or
components were as parts of a whole process which may or may not have
been related to each other, but definitely related to the whole.
Three components were of primary interest; a) the time from seeding
to first bloom, b) from first bloom to first fruit set, and c) first
fruit set to first ripe fruit. For added information two other
components were recorded, these were; d) time between first bloom
of the first inflorescence and the first bloom of the second, this
component was also called time between inflorescences, and finally
e) time from the first bloom of the second inflorescence to first

fruit set of this inflorescence. This latter component was recorded for purpose of comparison with the earlier component taken on the first inflorescence. Each component was measured in days and was determined independently for individual plants. This necessitated daily examination of each plant throughout the season of maturation. It was felt that each component was distinct enough to be analyzed separately and practically no re-grouping was attempted.

The components were defined as time intervals or stages whose limits could be easily recognized. This was important for keeping judgement errors to a minimum. The flower of the tomato literally springs open so that there was no difficulty in assessing a date of bloom. The ripe fruit was easily recognized and at first indication of color the plant was noted as mature. The most difficult and least precise measurement was that made of fruit set. Fruit set was defined as complete when the corolla of the flower appeared bleached out and wilting. This was readily identified in plants with simple and well formed flowers and with increasing difficulty in plants whose flowers had large and laterally compressed ovaries and pistils. For the most part its occurence was sudden, so that in any one day few intermediates could be found.

As it took from four to twelve man hours daily through the season to observe each plant caution was taken not to set any pattern for time of plot or man to plot in recording the data. However, each experiment was examined in as short a period of time as possible and completed before moving on to the next. Early in the season when work was slow the two men worked side by side to formulate procedures for

identification which were checked upon from time to time by consultation throughout the period of data taking - 114 field days, ie. June 3rd to September 24th. A plentiful supply of top grade fruits was apparently enjoyed by many.

6. Computations

As the data for each component were completed they were subjected to the planned statistical analysis outlined earlier in this section. It soon became apparent that it would take many months to complete the analyses on a desk calculator. The more routine analyses were then subjected to computer programming and used on the machines of the Departments of Physics and Mathematics, and Animal Husbandry of the Ontario Agricultural College. Some of the preliminary work of 1962 was processed at the McLennan Laboratory in the University of Toronto.

RESULTS

## 1. First Experiment

### Markers of chromosome number two

Currence (1938) reported that earliness in tomatoes as measured from time of seeding to first ripe fruit was under the genetic control of chromosome number two. The Yellow Cherry and Fireball varieties were selected for their earliness and crossed with late lines containing chromosome two markers. The markers were expressed phenotypically only in the homozygous state. In addition to having been coupled with one another, the marker genes were also coupled with the lateness genes for which the lines were selected. The early parent on the other hand consisted of the normal (+) gene for each marker and the early genes as well.

The results of these crosses are tabulated for each component separately and are presented in tables 3 to 5. The difference between parents is significant for each component in its expression of maturity and there exists a clear segregation of time intervals corresponding to certain markers. There are differences of 8 to 11 days between parents for the component first bloom, 1 and 2 days for fruit set, and 22 to 27 days for ripe fruit. Of the total difference in maturity between early and late parents (from 33 to 40 days) an average 67% is contributed by the component ripe fruit, less than 4% by fruit set, and the remaining 29% or so by the component first

- 22 -

Table 3A.   Segregation of earliness in days with markers of chromosome two in the cross 1) Yellow Cherry (early) X m d p o s (late)

| Generations and segregating classes | No. of plants | First bloom | Fruit set | Ripe fruit |
|---|---|---|---|---|
| $P_E$ early parent | 30 | 48.4 ± .23 | 3.5 ± .12 | 41.3 ± .29 |
| $P_L$ late parent | 30 | 56.6 ± .69 | 4.4 ± .24 | 65.1 ± 1.48 |
| $F_1$ hybrid | 30 | 49.7 ± .30 | 4.1 ± .12 | 40.5 ± .50 |
| $B_L$ testcross | 104 | 51.7 ± .39 | 3.9 ± .13 | 52.0 ± 1.01 |
| + + + + + | 24 | 51.5 ± .59 | 3.5 ± .17 | 44.4 ± 1.00 |
| + + + + s | 18 | 47.2 | 4.3 | 46.7 |
| + + + o + | 8 | 51.5 | 3.3 | 46.0 |
| + + p + + | 1 | 53.0 | 3.0 | 46.0 |
| + + p + s | 4 | 50.5 | 3.8 | 50.3 |
| + + p o + | 2 | 49.0 | 3.0 | 44.0 |
| + + p o s | 2 | 45.5 | 5.0 | 46.0 |
| m + + + + | 1 | 54.0 | 4.0 | 72.0 |
| m + + o + | 1 | 54.0 | 4.0 | 65.0 |
| m d + + + | 2 | 56.5 | 4.0 | 53.0 |
| m d p + + | 8 | 52.5 | 4.9 | 55.5 |
| m d p + s | 2 | 55.5 | 3.0 | 61.5 |
| m d p o + | 20 | 54.1 | 4.1 | 60.2 |
| m d p o s | 11 | 54.8 ± 1.78 | 4.1 ± .39 | 63.3 ± 4.09 |

Classes may be taken to express genotype of markers, e.g. + + + + + is equivalent to the genotype $\frac{M\ D\ P\ O\ S}{m\ d\ p\ o\ s}$ .

Table 3B.  Segregation of earliness in days with markers of chromosome two in the cross 1) Yellow Cherry (early) X m d p o s (late)

| Generations and segregating classes | No. of plants | Components | |
|---|---|---|---|
| | | Inflorescences | Fruit set 2 |
| $P_E$ early parent | 30 | $6.9 \pm .13$ | $2.9 \pm .13$ |
| $P_L$ late parent | 30 | $12.0 \pm .61$ | $4.9 \pm .18$ |
| $F_1$ hybrid | 30 | $6.9 \pm .21$ | $2.9 \pm .15$ |
| $B_L$ testcross | 104 | $8.4 \pm .28$ | $3.4 \pm .10$ |
| + + + + + | 24 | $6.7 \pm .34$ | $2.7 \pm .13$ |
| + + + + s | 18 | 9.1 | 3.7 |
| + + + o + | 8 | 6.1 | 3.0 |
| + + p + + | 1 | 6.0 | 2.0 |
| + + p + s | 4 | 8.8 | 3.0 |
| + + p o + | 2 | 7.5 | 2.5 |
| + + p o s | 2 | 11.0 | 4.0 |
| m + + + + | 1 | 7.0 | 4.0 |
| m + + o + | 1 | 7.0 | 3.0 |
| m d + + + | 2 | 8.8 | 6.0 |
| m d p + + | 8 | 7.5 | 3.4 |
| m d p + s | 2 | 8.0 | 5.0 |
| m d p o + | 20 | 9.3 | 4.0 |
| m d p o s | 11 | $10.7 \pm 1.22$ | $3.6 \pm .36$ |

Table 4.    Segregation of earliness in days with markers of chromosome
two in the cross 2) Yellow Cherry (early) X m d p aw o (late)

| Generations and segregating classes | No. of plants | Components | | |
|---|---|---|---|---|
| | | First bloom | Fruit set | Ripe fruit |
| $P_E$ early parent | 30 | 48.4 ± .23 | 3.5 ± .12 | 41.3 ± .28 |
| $P_L$ late parent | 30 | 59.8 ± .40 | 5.5 ± .23 | 68.3 ± 1.59 |
| $F_1$ hybrid | 30 | 51.5 ± .44 | 3.8 ± .14 | 39.2 ± .45 |
| $B_L$ testcross | 128 | 56.3 ± .28 | 4.2 ± .10 | 51.4 ± 1.07 |
| + + + + + | 48 | 54.5 ± .35 | 3.8 ± .15 | 41.7 ± .39 |
| + + + + o | 11 | 54.6 | 4.0 | 42.1 |
| + + + aw + | 3 | 51.7 | 3.7 | 39.0 |
| + + + aw o | 8 | 54.4 | 3.8 | 45.4 |
| + + p + o | 1 | 56.0 | 4.0 | 45.0 |
| m + + + + | 1 | 54.0 | 5.0 | 54.0 |
| m + + + o | 1 | 59.0 | 4.0 | 54.0 |
| m d + + + | 4 | 58.0 | 3.8 | 63.5 |
| m d + + o | 2 | 55.5 | 5.0 | 61.5 |
| m d + aw o | 1 | 55.0 | 5.0 | 58.0 |
| m d p + + | 3 | 57.3 | 4.0 | 58.7 |
| m d p + o | 3 | 60.7 | 4.3 | 66.0 |
| m d p aw+ | 1 | 60.0 | 3.0 | 60.0 |
| m d p aw o | 41 | 59.1 ± .36 | 5.0 ± .16 | 63.8 ± 1.48 |

Table 5.    Segregation of earliness in days with markers of chromosome two in the cross 3) Fireball (early) X m d p aw o (late)

| Generations and segregating classes | No. of plants | Components | | |
|---|---|---|---|---|
| | | First bloom | Fruit set | Ripe fruit |
| $P_E$ early parent | 30 | 50.1 ± .34 | 4.5 ± .15 | 46.5 ± .62 |
| $P_L$ late parent | 30 | 59.8 ± .40 | 5.5 ± .23 | 68.3 ± 1.60 |
| $F_1$ hybrid | 30 | 52.6 ± .52 | 4.2 ± .20 | 49.8 ± .74 |
| $B_L$ testcross | 152 | 55.3 ± .26 | 4.8 ± .11 | 58.6 ± .82 |
| + + + + + | 61 | 53.7 ± .32 | 4.3 ± .14 | 50.8 ± .71 |
| + + + + o | 12 | 53.3 | 3.8 | 49.8 |
| + + + aw o | 4 | 56.5 | 4.8 | 58.8 |
| + + p + + | 2 | 52.5 | 6.0 | 58.0 |
| + + p + o | 1 | 51.0 | 3.0 | 48.0 |
| + + p aw + | 1 | 55.0 | 4.0 | 58.0 |
| + + p aw o | 3 | 55.0 | 3.3 | 54.7 |
| + d + aw o | 1 | 57.0 | 5.0 | 63.0 |
| + d p + + | 1 | 61.0 | 6.0 | 71.0 |
| m + + + + | 1 | 59.0 | 4.0 | 74.0 |
| m d + aw + | 1 | 53.0 | 6.0 | 77.0 |
| m d + aw o | 4 | 56.0 | 5.3 | 62.8 |
| m d p + + | 3 | 71.0 | 4.3 | 65.3 |
| m d p + o | 1 | 53.0 | 6.0 | 72.0 |
| m d p aw o | 56 | 57.3 ± .40 | 5.5 ± .15 | 67.6 ± .88 |

bloom. Of the parents m d p aw o was 7 days later than m d p o s on the average and Fireball 8 days later than Yellow Cherry. The discrepancies between the two late parents and between the two early parents were approximately of the same magnitude for each component percentagewise as those given for the totals (tables 3 to 5).

It can be seen from tables 3 to 5 that in general the mean of the parents and generations fall into the order $P_E$, $F_1$, $B_L$, and $P_L$, that is from early parent to late parent. $F_1$ plants consist of half of the genome of each parent and where the early genes are concentrated in one parent and the late genes in the other parent the mean of the $F_1$ should be somewhere between the parent means. The exact position of the $F_1$ in relation to the parents depends on the degree of dominance. With overdominance or hybrid vigor the $F_1$ mean can exceed the parent mean. However, only when the $F_1$ mean is significantly earlier than the early parent or later than the late parent are hybrid vigor and overdominance invoked as causes. The $B_L$ mean is expected to fall between the $F_1$ mean and $P_L$ mean for the same reasons.

Similarities between $F_1$'s and their early parents suggests a large degree of dominance for earliness. The exception appearing in table 3A under fruit set is not consistent with the information provided in the testcross generation. It is expected that the backcross of the $F_1$ to the late parent should have a value between the $F_1$ and the $P_1$, but here it lies between the $F_1$ and the early parent. Furthermore, the testcross class + + + + + is as early as the early parent. For the marker genes this class is genotypically similar to the $F_1$ and if earliness genes are present in a fashion similar to Currence's find-

ings (1938) the observed value of 4.1 days for the $F_1$ must be a chance deviate. (See also top three comparisons in table 7).

The evidence presented supports three general hypotheses: 1) maturity in terms of earliness is heritable, 2) under the scale used a large degree of dominance for earliness exists, and 3) the components are justifiable in that they exhibit differences between parents though not necessarily among each other.

The results appearing in the tables 3 to 5 can be expanded after the methods of Currence (1938) in tomatoes, Gilbert (1960) in Drosophila and others, to yield correlated time measurements with gene markers. This allows an evaluation of chromosomal regions, in terms of days, as delimited by the markers. As an example of the procedure, the influence of the region of the chromosome marked with the recessive gene o (ovate fruit) for first bloom will be calculated from the phenotypic classes found in table 3A. Six comparisons are possible

1)  m + + + + (1) - m + + o + (1) = 0.00 days
2)  + + p + s (4) - + + p o s (2) = 5.00 days
3)  + + p + + (1) - + + p o + (2) = 4.00 days
4)  + + + + + (24) - + + + o + (8) = 0.00 days
5)  m d p + + (8) - m d p o + (20) = -1.60 days
6)  m d p + s (2) - m d p o s (11) = -3.32 days

The comparisons of the phenotypes differ only in the character o (ovate fruit). The plus symbol designates the normal and dominant condition and since this is testcross material the phenotypes represent abbreviated forms of the genotypes. Therefore, all plus (+) loci are heterozygous and all loci designated by an alphabetic symbol are homozygous recessive.

Large discrepancies clearly exist between the comparisons.

However, not all comparisons are equally trustworthy. The number in brackets gives the total number of plants recorded with the corresponding phenotype and some are represented by a single observation. A weighted average is calculated from the comparisons and the weight of each is determined by the lesser number of plants involved. This method then assesses lines 4) and 5) equal weights of 8, lines 2) and 6) weights of 2, and so on. The final estimate is -0.25 with a standard error of differences of $\pm$ .514. This value is entered in table 6 as -0.3 days. In this case it is clear that the "o" region has little or no influence on maturity time and of course it infers that the "$+^o$" region of the early chromosome contains no earliness genes.
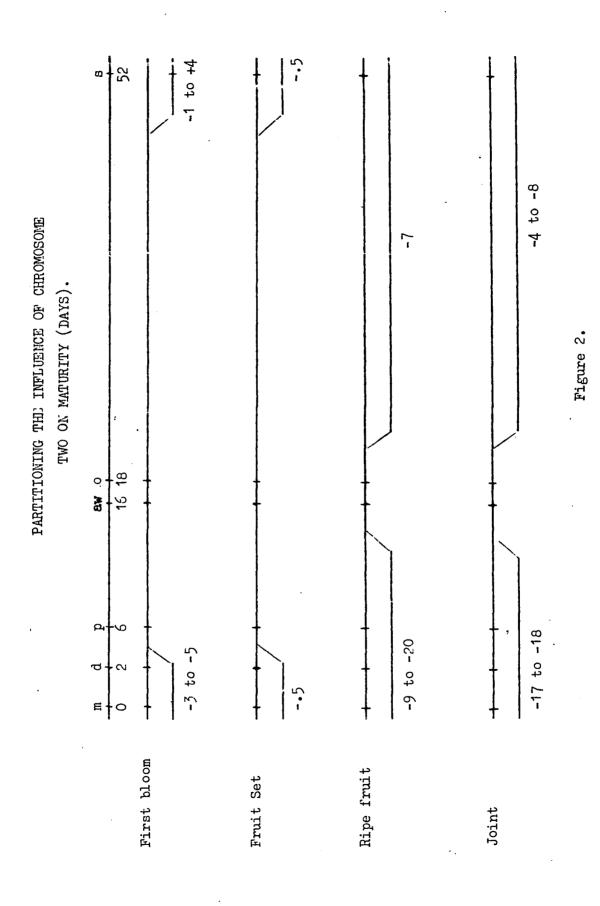
The Behren's-Fisher test is used to determine the significance of mean differences. The chosen level of probability for rejecting the null hypothesis is that of 1 in 20 or smaller. The Behrens-Fisher t test with its calculated degrees of freedom can be found in most texts of statistics.

The statistically meaningful values of table 6 are incorporated into the representation of figure 2. Each datum in the table is the result of a grouped and weighted analysis. Still certain values must be unreliable in that they are derived from few observations. The mutants mottled (m) and dwarf (d) are so closely linked, about 2 crossover units, that plants exhibiting one without the other are rare. Considering mottled and dwarf together as the "m-d" region is therefore, more reliable with a greater number of observations. The same is true in crosses with m d p aw o for green stem (aw) and ovate (o), which are also approximately 2 crossover units apart. It is convenient for the

Table 6. Average maturity in days per marker of chromosome two and of intervals between markers

| Cross identification and components | Markers and intervals | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | m | m-d | d | d-p | p | p-o | o | o-s | s |
| 1) Y.C. x m d p o s | (32-2) | (33-43) | (1-2) | (2-28) | (52-15) | (44-24) | (40-44) | (9-13) | (55-27) |
| First bloom | -2.5 | -5.4* | -2.5 | +0.7 | -0.2 | +2.2* | -0.3 | -1.1 | +2.3* |
| Fruit set | -0.6 | -0.2 | 0.0 | -0.5 | +0.2 | -0.1 | +0.2 | +0.5 | -0.4* |
| Ripe fruit | -23.3* | -12.9* | +19.0 | +10.7* | -1.9 | -2.9* | -1.7 | -6.9* | -2.8 |
| Inflorescences | -0.6 | -0.6 | -0.5 | -2.0 | -0.1 | -1.5* | -0.5 | -2.3* | -1.6* |
| Fruit set 2 | -0.7 | -1.6* | -2.0 | -0.2 | +1.1* | +0.7* | -0.3 | -0.4 | -0.7* |

| | m | m-d | d | d-p | p | p-aw | aw | aw-o | o |
|---|---|---|---|---|---|---|---|---|---|
| 2) Y.C. X m d p aw o | (59-2) | (68-10) | (2-6) | (2-6) | (18-48) | (6-42) | (67-54) | (55-50) | (60-66) |
| First bloom | -1.9 | -2.6* | -0.3 | -2.5 | -2.0* | -3.1* | +0.8* | -0.1 | -0.9* |
| Fruit set | -0.6 | -0.5* | +0.1 | +0.3 | +0.1 | +0.3 | +0.1 | -0.3* | -0.4* |
| Ripe fruit | -12.1* | -20.0* | -8.5 | -8.3 | -0.5 | -0.4 | -1.0 | -3.3* | -2.2 |
| 3) R X m d p aw o | (63-8) | (10-64) | (6-2) | (62-4) | (81-62) | (73-4) | (16-64) | (66-63) | (68-21) |
| First bloom | -4.8* | -4.4* | -4.5 | -9.7* | +0.5 | -1.6* | -3.4* | +2.8* | +1.7* |
| Fruit set | +0.6 | -0.8* | -0.1 | -1.0 | +0.7* | +0.5* | -0.2 | +0.2 | +0.6* |
| Ripe fruit | -5.7* | -8.5* | -8.6 | -5.8* | -2.0* | -5.5* | -5.5* | -3.1* | +1.2 |

* significant of chosen alpha = .05

(0-0) number of observations ie. no. of normal plants - no. of mutant plants.

- 30 -

PARTITIONING THE INFLUENCE OF CHROMOSOME

TWO ON MATURITY (DAYS).



Figure 2.

purpose of this experiment to consider chromosome two as having the regions; mottled-dwarf or "m-d", peach or "p", green stem-ovate or "aw-o", and compound or "s".

The chromosome map given in figure 2 measures 52 map units between mottled and compound and 50 units between dwarf and compound. Taken separately, however, dwarf and compound have about 30 crossover units separating them. Distances of 30 or more units of crossover are not easily detected in quantitative genetics (Mather, 1949). On the basis of this it may not be justifiable to divide the chromosome as it is delimited by the markers into more than two regions. With a greater number of observations in crossover classes the difficulty of dividing the chromosome into finer regions could be largely overcome. As it stands only ovate and compound has sufficient observations of crossing-over between them, 55 such observations. The "m-d" and "aw-o" has 25 crossover classes in the cross given in table 3. All map and crossover distances are taken from Butler (1960).

Examination of the significant (marked with an asterisk) values in table 6 supports the general contention that there are influences on maturity at both extremities of the marked chromosome. That there is more than one region influencing maturity is supported by the fact that the central portion, that of ovate in the cross Yellow Cherry with m d p o s is free of influence.

The component first bloom in the first cross is two days later for the "s" region and 5 days earlier for the "m-d" region. The results found in the interval between peach and ovate are not consistent with those in the other two crosses (table 6). The negative values given

for the same region for the second and third crosses must be remnant effects of the "m-d" region since 230 of the 280 chromosomes studied (tables 4 and 5) are intact for the section m d p aw o. As noted earlier the difference between parents of the first and third crosses are quite similar. It is difficult to resolve why in the second cross (table 6) the earlier of the early parents and the later of the late parents yield smaller differences in the comparisons of segregating classes. Unless the differences between the late lines are due to other than chromosome two influence, it may be due to crossing over rates differing in the various crosses. Only 20% of the marked chromosome of the third cross (table 5) showed some crossing over while 33% showed crossing over in the second cross (table 4). If this differential crossover frequency persists throughout the second chromosome for each cross, it would be expected that more crossovers between maturity genes outside the marked region and the gene markers would result in the second cross. In the second cross then there would be 13% more early alleles offset by the late alleles normally coupled with the m d p aw o markers.

The peculiar observations mentioned above do not leave the components fruit set and ripe fruit free of similar difficulties. Whereas first bloom exhibited -4 to -5 days of influence in the "m-d" region and +2 days in the "s" region, the component fruit set are quite equivalent for the two regions at -0.5 day each.

The expression of earliness in the component ripe fruit is such that it is difficult to allocate to a short region of the chromosome. There are indications that the sources are probably outside the marked chromosome section at the mottled end and between ovate and

compound at the compound end. It is at present impossible to search out the area outside mottled as the known terminal marker is only one additional c.o. unit. (Butler, 1960; Moens and Butler, 1963). Considering all three crosses together (table 6) the component ripe fruit contributes about 21 days (figure 2) to maturity. This is somewhat short of the 22 to 27 days difference between the parents for this component as mentioned earlier. The most plausible reason for this discrepancy is that the center of influence for the most intense region (as measured by "m-d" to be 14 days) is outside the marked region of the chromosome. This is supported by Currence's (1938) work where he found he could derive early strains of d p o s by repeated backcrossing, and could not markedly improve earliness except by selecting chromosome two markers.

Combining the components as in figure 2 give values which we are able to compare with those of Currence (1938). He found 13 days of influence for the dwarf region and 6 days in the compound region. The five day difference in the dwarf region can probably be accounted for by 1) pleiotropy of mottled and maturity, or 2) closer association of mottled than is dwarf with the late maturity genes.

## Interaction

The example given above for the determination of the influence of ovate on maturity provided six comparisons and the values obtained varied markedly. Since none of the comparisons had 10 or more observations for both classes tests of significance were not calculated except for the grouped estimate. Thus the six comparisons were termed

not significantly different from one another. Only with the marker
compound inflorescence (s) was it possible to completely evaluate some
of the comparisons. Currence (1938) found that the earliness expressed
by the compound region of the chromosome did not behave additively with
the dwarf region. Similar findings are reported here in table 7. A
sufficient number of observations is recorded in lines 4 and 8 of table
7 under the heading "Comparisons" to warrant separate tests of significance.
With additivity between regions of the chromosome it is expected that
all genotypic comparisons would yield similar values. Where such
values differ significantly the discrepancy is termed to be due to
interaction. Except for the component ripe fruit the values of lines
4 and 8 are not comparable as measured by their difference and tested
as interaction. Though interaction is prevalent its nature or mechanism
is not consistent through the individual components. This suggests
that although it is a interloci interaction it is not free of environmental
influence. This suggestion is reached from the assumption that the
genotypes per plant are constant through all components and only the
environment is not constant during the process of maturation. In
terms of the markers the interaction is expressed as a homozygous "s"
region with a heterozygous "m-d" region. Powers, Locke, and Garrett
(1950) included epistasis in their model and study of earliness.

Discrepancies and similarities between the genotypes of non-
segregating generations and similar testcross genotypic classes are
included in table 7 as well as differences between parents per component.

Table 7.  Interaction of "s" and "m-d" regions of the number two chromosome

| Comparisons | | Components | | | | |
|---|---|---|---|---|---|---|
| | | First bloom | Fruit set | Ripe fruit | Inflor. | Fruit set 2 |
| $P_E$ (30) - $P_L$ (30) = | | -8.20* | -0.93 | -23.77* | -5.10* | -1.97* |
| $F_1$ (30) - + + + + (24) = | | -1.83* | +0.57* | -3.89* | +0.19 | +0.22 |
| $P_L$ (30) - m d p o s (11) = | | +1.75 | +0.34 | +1.83 | +1.27 | +1.32* |
| + + + + (24) - + + + + s (18) = | | +4.28* | -0.78* | -2.30* | -2.35* | -1.01* |
| + + p + + (1) - + + p + s (4) = | | +2.50 | -0.75 | -4.25 | -2.75 | -1.00 |
| + + p o + (2) - + + p o s (2) = | | +5.50 | -2.00 | -2.00 | -3.50 | -1.50 |
| m d p + + (8) - m d p + s (2) = | | -3.00 | +1.88 | -6.00 | +0.75 | -1.62 |
| m d p o + (20) - m d p o s (11) = | | -0.72* | +0.01 | -3.07* | -0.48 | +0.40 |
| Total = | | +2.25* | -0.44* | -2.81 | -1.64* | -0.65* |
| Standard error of difference = | | ±.600 | ±.201 | ±1.558 | ±.415 | ±.146 |
| Interaction = | | +5.00* | -0.79* | +0.77 | -1.87* | -1.41* |
| Standard error of difference = | | ±.692 | ±.224 | ±1.880 | ±.482 | ±.210 |

* significant at chosen alpha = .05, calculated only when number of observations exceeds ten, and only then is interaction measured.

- 36 -

## Other gene markers

An assortment of markers was introduced by the late lines 49:75 and 3213. These were crossed with the same early parents used with the chromosome two marker lines, Yellow Cherry and Fireball. The results are recorded in table 8.

Association between brachytic (br) and colorless epidermis (y) are tested to be significant while most other gene markers appear to be independent (see table 2). The markers al, d, f, j, wt, and H are common to one cross and the monohybrid ratio of + to wt is significantly different from a one to one ratio. Only 5 of the 20 wilty plants are associated with dwarf and this may account for an accumulated influence of 10 days. Fasciation (f) has some effect and is probably pleiotropic. The markers jointless (j) and anthocyanin loser (al) show no significant association with wilty. The effects of jointless are probably also pleiotropic.

From the work presented by Currence (1938) and from this study, it is safe to regard the major effects of maturity as being on chromosome two. This doesn't deny the existence of other influences throughout the genome, but that if they do exist free of qualitative mutants they have yet to be detected and, therefore, would most likely play a minor role.

In summary this experiment supports the hypotheses: 1) that maturity is inherited at least in part, 2) the phase earliness is partially dominant to lateness and, 3) the components are distinct

Table 8.  Segregation of earliness in days with reference to a random selection of genetic markers

| Marker | Chromosome No. | No. of Plants | | Components | | |
|---|---|---|---|---|---|---|
| | | N | M | First Bloom | Fruit set | Ripe Fruit |
| r | 3 | 19 | 22 | -2.4 ± .45* | -0.1 ± .21 | -1.0 ± 1.86 |
| br | 1 | 34 | 29 | +0.8 ± .48 | +0.1 ± .16 | +0.1 ± 1.05 |
| y | 1 | 36 | 27 | +0.1 ± .48 | +0.3 ± .16 | +2.0 ± 1.04 |
| wf | 3 | 31 | 32 | -0.1 ± .41 | 0.0 ± .16 | +0.1 ± 1.05 |
| c | 6 | 21 | 24 | +0.5 ± .67 | +0.3 ± .27 | -1.7 ± .95 |
| gs | 7 | 9 | 36 | -0.5 ± .63 | +0.1 ± .24 | +2.6 ± .91 |
| d | 2 | 26 | 37 | -3.5 ± .48* | -0.8 ± .17* | -5.7 ± 1.02* |
| f | 11 | 38 | 36 | -0.9 ± .83 | -0.3 ± .17 | -4.1 ± 1.11* |
| j | 11 | 41 | 33 | -4.1 ± .77* | +0.2 ± .18 | -1.7 ± 1.17 |
| wt | 5 | 54 | 20 | +1.9 ± .82* | +0.1 ± .18 | -1.4 ± 1.17 |
| H | 10 | 37 | 37 | +0.4 ± .85 | -0.1 ± .18 | 0.0 ± 1.14 |
| al | 8 | 39 | 35 | -2.1 ± .84* | -0.2 ± .17 | -2.6 ± 1.14* |
| sp | 6 | 90 | 38 | interval between inflor. only | | |
| n | | | | | +1.6 ± .58* | |

N  normal

M  mutant

enough to justify their use. It also supports the contentions that two unequal size genes (or regions of unequal influence) which are on chromosome two control maturity in its major responses; that these two genes or regions are similar throughout the components, and that with the scale in use there is epistasis as expressed by interaction between the two loci. These interactions are not free of the influence of the environment and their nature changes in the time process of maturation.

## 2. Second experiment

Constant parent regression techniques as developed by Griffing (1950) and presented by Burdick (1954) are employed throughout this experiment to study gene action and interaction.

The basic mathematical method involves holding one of the parents constant and regressing the mean of the $F_1$ on the mean of the non-recurrent parent. The statistics calculated in this manner, holding each parent constant in turn, are called the constant parent regression coefficients (C.P.R.), and their means, constant parent series (C.P.S.).

The method can be best illustrated by the construction of models. The simplest model would involve a character controlled by a single locus. A monogenic character at best would account for only three classes. The data presented in this section shows four and five distinct classes (table 9) so the one locus representation will be omitted. The next simplest model would be one with two loci and with no dominance or epistasis. In all cases absence of linkage will be assumed. However, this is not a necessary assumption in these methods as they do not involve segregating classes. With inbred parents the four genotypes AABB, AAbb, aaBB, and aabb are the only possibilities with

two loci. The six possible types of matings, ignoring reciprocals, and their values when A=B=0 and a=b=1 are:

|  | C.P.R. | C.P.S. | aabb | aaBB | AAbb | AABB |
|---|---|---|---|---|---|---|
| AABB | .500 | 1.00 | 2 | 1 | 1 | 0 |
| AAbb | .500 | 2.00 | 3 | 2 | 2 | |
| aaBB | .500 | 2.00 | 3 | 2 | | |
| aabb | .500 | 3.00 | 4 | | | |

An example of the calculations for deriving the C.P.R. coefficient follows: holding the parent AABB constant its C.P.R. coefficient

becomes $\dfrac{(1)(2)+(1)(2)+(2)(4)-[(1+1+2)(2+2+4)/3]}{2^2+2^2+4^2-[(2+2+4)^2/3]} = \dfrac{1\ 1/3}{2\ 2/3} = .5.$

The constant parent series (C.P.S.) is the mean value of the constant parent and its hybrids. Further, it is possible to calculate a second order regression coefficient $(b_2)$ by regressing the C.P.R.'s on the parents. In this model $b_2$ would equal zero.

With two loci, complete dominance, and no epistasis the model takes the form:

|  | C.P.R. | C.P.S. | aabb | aaBB | AAbb | AABB |
|---|---|---|---|---|---|---|
| AABB | .000 | 0.00 | 0 | 0 | 0 | 0 |
| AAbb | .286 | 1.00 | 2 | 0 | 2 | |
| aaBB | .714 | 2.00 | 2 | 2 | | |
| aabb | 1.000 | 3.00 | 4 | | | |

$b_2 = .25$

$\overline{X} = .00$

$\overline{X}$ is calculated from the regression equation with $b_2$ when $\overline{Y}$, an estimate of the constant parent regression coefficient (C.P.R.), is equal to zero. $\overline{X}$ is interpreted as an estimate of the value of a parent homozygous dominant at all loci expressed in the model without over-

dominance.

Models with complete epistasis would contain only two classes of parents and under the present system the C.P.R.'s would all equal zero. Omitting epistasis of the type where a homozygous locus interacts with another homozygous locus, it would be possible for the parents to have more than two values. Whether there is dominance or not, however, would result in all hybrids being equal to zero. This would result in the C.P.R.'s being zero also.

Of interest are models where the A locus is not equal to the B locus: given a = 2, b = 1, A = B = 0 with no epistasis the model would be similar to the first one constructed, but the 4 parents would differ in value. On the other hand: given a = 2, b = 1, A = B = 0 and complete dominance,

|      | C.P.R. | C.P.S. | aabb | aaBB | AAbb | AABB |
|------|--------|--------|------|------|------|------|
| AABB | .000   | .00    | 0    | 0    | 0    | 0    |
| AAbb | .286   | 1.00   | 2    | 0    | 2    |      |
| aaBB | .714   | 2.00   | 4    | 4    |      |      |
| aabb | 1.000  | 3.00   | 6    |      |      |      |

$$b_2 = 1.71$$
$$\overline{X} = .076$$

In this model an epistasis of the type heterozygous x heterozygous could not be detected. Epistasis of a homozygous x heterozygous type would make all hybrids equal to zero. The various types of epistasis in the two loci models are more difficult to detect when dominance is nearly complete. However, only a few cases have been illustrated here to serve as a guide. Epistasis can be expected to be more clearly expressed in experiments including segregating generations. The fact that the illustrations presented disregarded the degree of effects is

al.. to be k.,.c in mind when they are put to use as aids to interpretating the experimental results.

Burdick (1949) in his doctoral dissertation generalized the model for epistasis and showed that a negative $b_2$ in the illustrations given above indicates genic interactions of unspecified nature.

The means of the seven varieties used as parents in this experiment are recorded in table 9. If all differred significantly from one another seven genotypes could be represented. In fact only four or five of the seven differ sufficiently to be noted as distinct.types. Under the conditions of the experiment it is doubtful if the range exhibited in the values of table 9 could be extended. Even if climatic conditions permitted extension of the range of values little would be gained. Powers, et al. (1950) reported later varieties, but these were grown in a comparatively arid area. Southern Ontario has a very good climate for growing tomatoes and rate of maturation to harvestable fruit is near excellent.

Table 9.   Means and standard errors of parent varieties

| Parents | Components | | | | |
|---|---|---|---|---|---|
| | First bloom | Fruit set | Ripe fruit | Inflor. | Fruit set 2 |
| Red Currant | 51.9 $\pm$ .39 | 3.5 $\pm$ .15 | 37.2 $\pm$ .72 | 5.5 $\pm$ .31 | 2.8 $\pm$ .11 |
| Yellow Cherry | 53.8 $\pm$ .30 | 3.1 $\pm$ .15 | 38.8 $\pm$ .58 | 4.3 $\pm$ .24 | 2.6 $\pm$ .15 |
| Fireball | 54.1 $\pm$ .35 | 4.1 $\pm$ .22 | 50.3 $\pm$ .88 | 4.7 $\pm$ .25 | 3.3 $\pm$ .31 |
| U.S.D.A. | 54.2 $\pm$ .71 | 6.1 $\pm$ .33 | 53.3 $\pm$ 1.28 | 8.7 $\pm$ .56 | 4.8 $\pm$ .09 |
| John Baer | 57.8 $\pm$ .54 | 3.0 $\pm$ .13 | 53.1 $\pm$ .89 | 6.6 $\pm$ .67 | 3.3 $\pm$ .49 |
| Rutgers | 61.1 $\pm$ .60 | 5.8 $\pm$ .31 | 56.5 $\pm$ 1.03 | 4.9 $\pm$ .83 | 5.8 $\pm$ .18 |
| Tangerine | 58.8 $\pm$ .13 | 3.9 $\pm$ .12 | 60.9 $\pm$ .98 | 8.2 $\pm$ .39 | 4.2 $\pm$ .22 |

Coefficients of correlation of plot means and plot variances within the parent varieties for each component are given in table 10. A significant correlation indicates the need for a transformation of the data to units giving no mean-variance correlation. Only the last component in the table indicates such a need. Being the only such case it did not appear urgent or meaningful to carry out such a transformation.

Table 10.   The mean-variance correlation coefficient r within parent
            varieties

| Component description | r |
| --- | --- |
| Days from seeding to first bloom | -.19 |
| Days from first bloom to fruit set | .40 |
| Days from fruit set to ripe fruit | .46 |
| Days between inflorescences | .34 |
| Days from first bloom to fruit set on the second inflorescence | .82* |

* significant at chosen alpha = .05

An analysis of the variance of each component is presented along with the results of the constant parent regression analyses in tables 11 through 15.

### The component first bloom

The results of the component first bloom, given in table 11B, are consistent with the partial dominance of earliness. An average dominance of 50% is calculated from the ratio $100(\overline{P} - \overline{F}_1) /(\overline{P} - \overline{F}_{II})$. Only two slopes, as depicted by the regression coefficients are significant, two others are of the same magnitude. The parents' means fall into four classes: 1) the earliest, Red Currant, 2) Yellow Cherry, Fireball,

Table 11A.  Analysis of variance of the component days from seeding to first bloom.

| SOURCE | D.F. | S.S. | F | |
|---|---|---|---|---|
| Total | 354 | 3229.32 | | |
| Subtotal | 119 | 2485.99 | | |
| Varieties | 29 | 2169.32 | 20.84 | p < .005 |
| Blocks | 3 | 3.97 | .37 | n.s. |
| Within Error | 87 | 312.70 | 1.14 | n.s. |
| Residual | 235 | 743.33 | | |

5 missing subplots

n.s.  not significant at chosen alpha = .05

Tangerine and Red Currant have an extra plot each

Table 11B.  Means in days for the 28 varieties and $F_1$'s

| | C.P.R. | C.P.S. | R. | T. | J.B. | U.S. | F. | Y.C. | R.C. |
|---|---|---|---|---|---|---|---|---|---|
| Red Currant | .3332 | 53.6 | 55.3 | 54.8 | 52.8 | 53.6 | 52.5 | 52.4 | 51.9 |
| Yellow Cherry | .2140 | 53.7 | 53.8 | 55.0 | 54.5 | 53.9 | 52.5 | 53.8 | |
| Fireball | .5719* | 54.8 | 57.1 | 57.0 | 54.6 | 53.3 | 51.1 | | |
| U.S.D.A. | .2774 | 54.4 | 56.3 | 55.0 | 54.0 | 54.2 | | | |
| John Baer | .6986* | 55.5 | 59.1 | 58.0 | 57.8 | | | | |
| Tangerine | .5074 | 56.5 | 59.2 | 58.8 | | | | | |
| Rutgers | .6895 | 56.8 | 61.1 | | | | | | |

$\overline{P} = 55.96$

$\overline{F}_1 = 54.99$

$\overline{F}_{II} = 53.98$

$b_2 = .0444$

$\overline{X} = 45.37$

\*  significant at chosen alpha = .05

C.P.R.  constant parent regression coefficient

C.P.S.  constant parent series

$\overline{P}$  observed means of parents

$\overline{F}_1$  observed mean of $F_1$'s

$\overline{F}_{II}$  expected mean of $F_1$'s on hypothesis of complete dominance

$b_2$  second degree regression coefficient

$\overline{X}$  hypothetical parent dominant homozygous at all loci

U.S.D.A., 3) John Baer, Tangerine, and 4) the latest, Rutgers. The C.P.R.'s support the hypothesis of one or two possible loci (see models) and the parents two or more loci (tables 9 and 11B), i.e. two loci if they are not equal in expression, more than two if the loci concerned are equal. The coefficient $b_2$ is not significant and, therefore, $\bar{X}$ is probably not reliable.

$\bar{F}_{II}$ represents the expected $F_1$ mean (over all hybrids) under the assumption of complete dominance of earliness. It is calculated after Burdick (1954) as $[F_{ab} + F_{ac} + \dots + F_{bc} + F_{bd} + \dots + F_{(n-1)n}]/$ $n(n-1)/2$, where $F_{ab}$ is the mean of the $F_1$ produced by parents a and b, and the values of the parents are in the order $a < b < c \dots < n$.

### The component fruit set

Fruit set as a component has disadvantages the other components have not. It has a duration of 3 to 6 days and an error judgement of one day becomes comparatively large. In addition it is more prone to errors as it is not as clearly delimited biologically as are the other components. The analysis of variance (table 12A) shows a significantly small F ratio for blocks. This points to some none randomness in the data. The other components do not have this so it is perhaps a chance phenomenon. The regression results (table 12B) show strong inconsistencies. Yellow Cherry appears significantly earlier than Red Currant and this should lead to similarly ranked C.P.R.'s. These are reversed and significantly so. The component fruit set 2 (table 15B) does not demonstrate such inconsistencies. Other striking dissimilarities between the two components are the values of the parents Fireball and U.S.D.A. Considering the analysis of variance (tables 12A and 15A) for

Table 12A.    Analysis of variance of the component days from first
bloom to fruit set

| SOURCE | D.F. | S.S. | F | |
|---|---|---|---|---|
| Total | 354 | 463.93 | | |
| Subtotal | 119 | 308.60 | | |
| Varieties | 29 | 244.85 | 11.56 | p < .005 |
| Blocks | 3 | .32 | .15 | p < .005 |
| Within Error | 87 | 63.43 | 1.11 | n.s. |
| Residual | 235 | 155.33 | | |

5 missing subplots

Table 12B.    Means in days for the 28 varieties and $F_1$'s

| | C.P.R. | C.P.S. | U.S. | R. | F. | T. | R.C. | Y.C. | J.B. |
|---|---|---|---|---|---|---|---|---|---|
| John Baer | .4356* | 3.5 | 4.5 | 3.8 | 3.3 | 2.8 | 3.6 | 2.8 | 3.0 |
| Yellow Cherry | .4170* | 3.4 | 4.3 | 3.7 | 3.0 | 3.3 | 3.0 | 3.1 | |
| Red Currant | .2167 | 3.4 | 4.3 | 3.3 | 3.3 | 2.9 | 3.5 | | |
| Tangerine | .3993* | 3.4 | 4.2 | 4.0 | 3.0 | 3.9 | | | |
| Fireball | .3056* | 3.4 | 4.1 | 3.9 | 4.1 | | | | |
| Rutgers | .5795* | 4.0 | 5.4 | 5.8 | | | | | |
| U.S.D.A. | .3555 | 4.5 | 6.1 | | | | | | |

$\overline{P}$ = 4.21
$\overline{F}_1$ = 3.64
$\overline{F}_{II}$ = 3.48
$b_2$ = .0298
$\overline{X}$ = -6.77

the two components, the state of the $b_2$ estimates (tables 12B and 15B), along with the unreasonable results of fruit set (table 12B), it will be largely overlooked in favor of component fruit set 2 (table 15B).

### The component ripe fruit

This is the last component measured during the field season. It is on the average one month later than the previous measurement. As the season progresses an increase incidence of abortion of the flowers and other hindrances which cause unripe fruit to drop prevent the accurate determination of this component. This is considered in the analysis of covariance (table 13A) of ripe fruit date on position of ripe fruit on the inflorescence. The means (table 13B) are adjusted by a factor of 3.8 days per truss.

The values obtained (table 13B) for the means of the parents, the C.P.R.'s, and the C.P.S.'s are in good agreement. The parent means (table 9) suggest that four and possibly five distinct classes exist. The C.P.S. values do not really distinguish between the parents Fireball, John Baer, and U.S.D.A. The C.P.R. coefficients could place U.S.D.A. as easily with Fireball or Rutgers as alone. The C.P.R.'s are so correlated according to Griffing (1948) that it is difficult to test between them. On the grounds that U.S.D.A. shows a degree of dominance very similar to Fireball it will be placed in that class. The results of this component compare favorably with the model illustrated under the mechanism of complete dominance and unequal loci effects. Average dominance is estimated at 96% by the ratio $100(\bar{P} - \bar{F}_1) / (\bar{P} - \bar{F}_{II})$. A significant second order regression coefficient $(b_2)$ allows an estimate of the most potent parent to be calculated at about 36.8 days. This is well within

Table 13A.  Analysis of covariance of the component days from fruit set to ripe fruit on position of ripe fruit

| SOURCE | D.F. | $Y^2$ | XY | $X^2$ | Adj.F | |
|---|---|---|---|---|---|---|
| Total | 353 | 31761.33 | 197.33 | 10.17 | | |
| Subtotal | 118 | 29629.33 | 160.73 | 5.10 | | |
| Varieties | 29 | 28513.91 | 145.53 | 2.08 | 89.76 | $p < .005$ |
| Blocks | 3 | 173.85 | 4.24 | .12 | 4.65 | $p < .01$ |
| Within Error | 86 | 941.56 | 10.96 | 2.91 | 1.27 | n.s. |
| Residual | 235 | 2132.00 | 36.60 | 5.07 | | |

$b = 3.77$  $p$  .05

5 missing subplots

Table 13B.  Means in days for the 28 varieties and $F_1$'s

| | C.P.R. | C.P.S. | T. | R. | U.S. | J.B. | F. | Y.C. | R.C. |
|---|---|---|---|---|---|---|---|---|---|
| Red Currant | -.0156 | 36.7 | 37.2 | 35.8 | 36.6 | 37.4 | 36.0 | 37.2 | 37.2 |
| Yellow Cherry | .0545 | 38.2 | 39.1 | 37.6 | 37.4 | 38.5 | 39.2 | 38.8 | |
| Fireball | .7969* | 47.4 | 54.5 | 53.5 | 50.4 | 50.8 | 50.3 | | |
| John Baer | .7469* | 47.4 | 53.3 | 53.5 | 50.7 | 53.1 | | | |
| U.S.D.A. | .8839* | 47.6 | 56.9 | 53.5 | 53.3 | | | | |
| Rutgers | .9536* | 48.4 | 56.3 | 56.5 | | | | | |
| Tangerine | 1.0711* | 49.6 | 60.9 | | | | | | |

$\overline{P} = 50.01$

$\overline{F}_1 = 45.02$

$\overline{F}_{II} = 44.80$

$b_2 = .0485*$

$\overline{X} = 36.78$

the variability of the Red Currant parent.

## Time between inflorescences

Difficulties of the very nature expressed in the data for component fruit set (table 12B) is in evidence for the time interval between inflorescences (table 14B). There exists no other comparable component, however, to check reliability. There is some evidence here for epistasis in that the $b_2$ is negative, but it is not significant. Dominance is estimated at 45%.

Two points of consideration prevent a conclusion of general epistasis for this component, 1) although only one C.P.R. is significant, others have large values, and 2) the parent classes are not clear, but there are probably as many as five.

## The component fruit set 2

This component was initially meant to supplement and not replace its earlier facsimile. Its reasonable results, however, make the switch desirable.

Average dominance is registered only at 43%, but Yellow Cherry, Red Currant, and Fireball clearly show much greater potence. The most potent parent estimate of 2.7 is very reasonable in the light of the parent means for Yellow Cherry and Red Currant. The model suggested is that used for the component ripe fruit. The two components compare well in rank of parent means, especially with the early parents. There is not much evidence to indicate that the two components do not operate by the same underlying genetic mechanisms.

Table 14A.  Analysis of variance of the component days between
inflorescences

| SOURCE | D.F. | S.S. | F | |
|---|---|---|---|---|
| Total | 354 | 1247.33 | | |
| Subtotal | 119 | 735.33 | | |
| Varieties | 29 | 522.25 | 7.44 | p < .005 |
| Blocks | 3 | 2.96 | .41 | n.s. |
| Within Error | 87 | 210.12 | 1.11 | n.s. |
| Residual | 235 | 512.00 | | |

5 missing subplots

Table 14B.    Means in days for the 28 varieties and $F_1$'s

| | C.P.R. | C.P.S. | U.S. | T. | J.B. | R.C. | R. | F. | Y.C. |
|---|---|---|---|---|---|---|---|---|---|
| Yellow Cherry | .0613 | 5.2 | 5.7 | 5.0 | 5.2 | 4.9 | 5.2 | 5.3 | 4.3 |
| Fireball | .4098 | 5.4 | 7.5 | 5.1 | 5.5 | 4.8 | 4.4 | 4.7 | |
| Rutgers | .5561* | 5.8 | 6.5 | 7.3 | 6.6 | 4.5 | 4.9 | | |
| Red Currant | .0490 | 4.9 | 5.0 | 4.8 | 5.3 | 5.5 | | | |
| John Baer | .2853 | 6.0 | 6.8 | 6.6 | 6.6 | | | | |
| Tangerine | .3549 | 6.0 | 6.9 | 8.2 | | | | | |
| U.S.D.A. | .1579 | 6.4 | 8.7 | | | | | | |

$\overline{P}$ = 6.13

$\overline{F}_1$ = 5.66

$\overline{F}_{II}$ = 5.08

$b_2$ = -.0073

$\overline{X}$ = 42.80

Table 15A. Analysis of variance of the component days from first bloom to fruit set on the 2nd inflorescence

| SOURCE | D.F. | S.S. | F | |
|---|---|---|---|---|
| Total | 354 | 547.72 | | |
| Subtotal | 119 | 395.05 | | |
| Varieties | 29 | 335.22 | 19.93 | p < .005 |
| Blocks | 3 | 9.43 | 5.41 | p < .005 |
| Within Error | 87 | 50.40 | .89 | n.s. |
| Residual | 235 | 152.67 | | |

5 missing subplots

Table 15B. Means in days for the 28 varieties and $F_1$'s

| | C.P.R. | C.P.S. | R. | U.S. | T. | J.B. | F. | R.C. | Y.C. |
|---|---|---|---|---|---|---|---|---|---|
| Yellow Cherry | .0331 | 2.7 | 2.7 | 3.0 | 2.4 | 2.6 | 3.1 | 2.5 | 2.6 |
| Red Currant | .1239 | 2.9 | 2.8 | 3.7 | 2.4 | 2.8 | 3.1 | 2.8 | |
| Fireball | .0154 | 3.4 | 2.8 | 3.7 | 4.1 | 3.3 | 3.3 | | |
| John Baer | .4543* | 3.4 | 4.0 | 4.0 | 3.7 | 3.3 | | | |
| Tangerine | .8146* | 3.7 | 5.3 | 4.3 | 4.2 | | | | |
| U.S.D.A. | .8383* | 4.1 | 6.0 | 4.8 | | | | | |
| Rutgers | 1.6179* | 3.9 | 5.8 | | | | | | |

$$\bar{P} = 3.83$$
$$\bar{F}_1 = 3.44$$
$$\bar{F}_{II} = 3.14$$
$$b_2 = .4806*$$
$$\bar{X} = 2.67$$

3. __Third experiment__

## Variance models

A method developed by Mather (1949) for the partitioning of variance provides the basic model for this experiment. The parameters D and H of the model, as presented in the introduction, are developed as quadratic forms of d and h. The d and h are linear measurements illustrated in figure 1 in a single locus representation. With the assumption that the quantitative system under study has additive loci effects, D and H become equivalent to $\Sigma(d^2)$ and $\Sigma(h^2)$, respectively.

Therefore, in the case of the individual locus the development from the two contrasting, but true breeding parents to the $F_2$ can be followed as such:

```
Parents      d    x    -d       i.e.    AA    x    aa
F₁                h                            Aa
F₂     1/4 d + 1/2 h - 1/4 d              AA : 2 Aa : aa
```

so that,

the mean of $F_2$: $\overline{F}_2 = 1/2\ h$

and with no epistasis summed over all loci,

the variance of $F_2$: $V_{F2} = (1/4\ d^2 + 1/2\ h^2 + 1/4\ d^2) - 1/4\ h^2$

$$= 1/2\ d^2 + 1/4\ h^2 + \text{an error term } E,$$

the $- 1/4\ h^2$ is the correction factor, i.e. $(\overline{F}_2)^2$. This becomes in Mather's terms $V_{F2} = 1/2\ D + 1/4\ H + E$.

The following can be derived in similar fashion:

$V_{\overline{F3}} = 1/2\ D + 1/16\ H + E$, i.e. variance of means of $F_3$ progenies derived from selfed $F_2$ plants.

$W_{F2/F3} = 1/2\ D + 1/8\ H$, i.e. covariance of $F_3$ mean on $F_2$ parent,

environmental effects supposedly cancelling each other.

$\overline{V}_{F3} = 1/4\ D + 1/8\ H + E$, i.e. the mean variance of all $F_3$ progenies.

It is important to note in this model that all descendant families are from selfed parents with the exception of the initial $F_1$ hybrid. The model can be expanded easily to cover biparental progenies but, it is not necessary to go further as it will not be representative of the work to be presented in this dissertation.

In dealing with variances it is particularly important that for unambiguous results an adequate scale be employed. This is important in order to render the effects of all loci additive to meet the assumption of the model. The additivity of a scale is largely determined by tests on means of generations. It is not sufficient to have these tests show only a minimum of departure from the desirable linear model, but it is also necessary to have stable variances. It is often necessary to compromise and select a scale which falls short in its tests of additivity as measured by generation means, but is stable in generation variances. Models employing interaction terms appear valuable in preventing such a dilemma. However, such a model with second-degree statistics would contain more unknowns than is possible to solve without the complete classification of the genotypes of the quantitative trait. Since this cannot always be achieved it leaves proper scaling an important factor in methods of partitioning variance.

The means, their standard errors as well as tests of additivity are presented in table 16 for calculations made on the arithmetic scale. For the three components of primary interest the calculations were re-

peated on a logrithmic scale and the results are recorded in table 17.

Table 16.   The mean number of days and the standard error for each component of maturity

| Generations and scaling tests | Components | | | | |
|---|---|---|---|---|---|
| | First bloom | Fruit set | Ripe fruit | Inflor. | Fruit Set 2. |
| Red Currant | $51.9 \pm .11$ | $3.5 \pm .05$ | $37.2 \pm .16$ | $5.8 \pm .08$ | $2.6 \pm .05$ |
| Tangerine | $59.3 \pm .10$ | $4.0 \pm .06$ | $56.8 \pm .24$ | $9.9 \pm .13$ | $4.4 \pm .07$ |
| $F_1$ | $54.7 \pm .18$ | $3.1 \pm .06$ | $38.1 \pm .19$ | $6.5 \pm .13$ | $2.5 \pm .08$ |
| $F_2$ | $54.4 \pm .14$ | $3.3 \pm .04$ | $39.9 \pm .15$ | $6.6 \pm .08$ | $2.9 \pm .04$ |
| $F_3$ | $54.8 \pm .10$ | $3.3 \pm .02$ | $42.6 \pm .14$ | $7.2 \pm .06$ | $3.1 \pm .02$ |
| $A_{\overline{F2}}$ | $-2.9 \pm .70*$ | $-0.7 \pm .23*$ | $-10.8 \pm .78*$ | $-2.3 \pm .44$ | $-0.6 \pm .25*$ |
| $A_{\overline{F3}}$ | $-4.8 \pm .96*$ | $-2.4 \pm .31*$ | $-11.7 \pm 1.45*$ | $-2.8 \pm .69$ | $-0.9 \pm .35*$ |
| $A_{\overline{F3}}'$ | $-0.9 \pm .51$ | $-0.9 \pm .15*$ | $-3.5 \pm .69*$ | $-0.3 \pm .33$ | $0.0 \pm .15$ |

* significant at chosen alpha = .05

$$A_{\overline{F2}} = 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_E - \overline{P}_L \text{ with } V_{A\overline{F2}} = 16 V_{\overline{F2}} + 4V_{\overline{F1}} + V_{\overline{PE}} + V_{\overline{PL}}$$

$$A_{\overline{F3}} = 8\overline{F}_3 - 2\overline{F}_1 - 3\overline{P}_E - 3\overline{P}_L \text{ with } V_{A\overline{F3}} = 64V_{\overline{F3}} + 4V_{\overline{F1}} + 9V_{\overline{PE}} + 9V_{\overline{PL}}$$

$$A_{\overline{F3}}' = 4\overline{F}_3 - 2\overline{F}_2 - \overline{P}_E - P_L \text{ with } V_{A\overline{F3}}' = 16 V_{\overline{F3}} + 4 V_{\overline{F2}} + V_{\overline{PE}} + V_{\overline{PL}}$$

The futility of finding a simple and adequate scale is apparent from these two tables.  For one thing, both scales fall far short of giving additivity to the generation means.  The significant departures of the A's (table 16) and Q's (table 17) from zero testify to this.  With only two exceptions, the deviations indicate the need for a transformation which will shorten the upper end of the distribution.  The second point to consider is that when a transformation such as to logarithms which shortens the upper end of the distribution is applied to the data, the

variances lose their stability and become quite erratic (table 17). A complete analysis of the component first bloom on the logrithmic scale did not give results which were any more trustworthy than those of the arithmetic scale and probably was less meaningful in biological terms. Under the circumstances it was decided to proceed with the partitioning of the variance on the original scale.

Table 17.  Means in $\log_e$ days (coded)

| Generations and scaling tests | Components | | |
| --- | --- | --- | --- |
| | First bloom | Fruit set | Ripe fruit |
| Red Currant | $2.466 \pm .010$ | $1.235 \pm .013$ | $1.888 \pm .031$ |
| Tangerine | $2.958 \pm .005$ | $1.369 \pm .016$ | $3.280 \pm .003$ |
| $F_1$ | $2.676 \pm .011$ | $1.106 \pm .022$ | $2.055 \pm .009$ |
| $F_2$ | $2.635 \pm .011$ | $1.128 \pm .014$ | $2.213 \pm .017$ |
| $F_3$ | $2.647 \pm .008$ | $1.147 \pm .008$ | $2.427 \pm .012$ |
| $Q_{\overline{F2}}$ | $-.238 \pm .053*$ | $-.305 \pm .075*$ | $-.425 \pm .077*$ |
| $Q_{\overline{F3}}$ | $-.442 \pm .076*$ | $-.852 \pm .096*$ | $-.197 \pm .135$ |
| $Q_{\overline{F3}}'$ | $-.102 \pm .040*$ | $-.273 \pm .069*$ | $.114 \pm .066$ |

$Q$ = A of table 16 after transforming each observation to $\log_e$

Each observation is reduced by 40 days in first bloom and 30 days in ripe fruit before transforming.

The design of the experiment explained in the section MATERIALS AND METHODS will be reviewed briefly here in an effort to demonstrate how it is related to the calculations. These calculations provide the direct estimates of generation variances and error terms.

The experiment consists of four blocks, each is identical with 100 plots of seven plants. The mean and variance of each plot is calculated. The variance of the $F_2$ and mean variance of the $F_3$ are calculated by taking the average variance of their 20 and 60 plots, respectively. Associated with $V_{F2}$ and $\overline{V}_{F3}$ is an error term ($E_1$) determined from within plots. This can be estimated directly from the average variances of the 20 parents and $F_1$ plots. The variance of the $F_3$ means is calculated from the 60 $F_3$ plot means and has a different error ($E_2$), one which is between plots. This can be estimated directly from the variance of the 20 parent and $F_1$ plot means. The covariance of the $F_3$ mean and the $F_2$ parent value is calculated between the 60 $F_3$ plot means of 1963 and the 60 parent plants of 1962. The least square estimate of $W_{F2/F3}$ has no error term. Each block is treated separately.

Six direct estimates are thus extracted from each experimental block to solve the four unknowns D, H, $E_1$ and $E_2$. These are submitted to the methods of linear algebra illustrated in Mather (1949) for solving simultaneous equations. This model is called the inclusive model (Inc.).

A crude test for detecting linkage between loci effecting the quantitative trait is available. Mather (1949) calls it a test for the homogeneity of D and H provided by the separate generations. $V_{F2}$, $V_{\overline{F3}}$ and $W_{F2/F3}$ are available for the estimation of D and H of the $F_2$ generation, while $\overline{V}_{F3}$ involves D and H of the $F_3$. With linkage the non-random distribution of the loci effecting the trait will increase variation disproportionately in the $F_2$ and $F_3$ generations and disturb the equivalence of D and H to $\Sigma(d^2)$ and $\Sigma(h^2)$, respectively. A divergence in the value of D and H, therefore, increases through

succeeding generations. It should be made clear that the test to be presented does not measure divergence between D and H, but rather of D and H between generations.

The estimates for D, H, $E_1$, and $E_2$ are recalculated omitting the direct estimate of $\overline{V}_{F3}$. Five rather than the six original equations are now available. If D and H have a different value in the $F_3$, then the new estimates D, H, $E_1$, and $E_2$ should differ from the original values of the parameters. This is called the exclusive model (Exc).

Theoretical values for the generations under the premises of each model are constructed and the differences between them attributed to linkage effects. An analysis of variance provides the test of significance for assessing the discrepancies between the two models.

Using the foregoing methods the results obtained for the components first bloom, fruit set, and ripe fruit are presented in tables 18, 19 and 20 respectively. Part A of these tables has four direct estimates for each of the six variances listed. Also included are the pooled estimates of the four blocks and the theoretical or expected values derived from the inclusive and exclusive models. It is now possible to submit the 24 basic statistics to an analysis of variance (part B of the tables).

From each of the 24 observed statistics, three deviations are calculated, 1) from the pooled estimate, 2) from the inclusive model, and 3) from the exclusive model. The deviations squared from the inclusive model estimates the total variance. The deviations squared from the exclusive model subtracted from the total variance gives the estimate of the variance due to linkage. The error is estimated by

Table 18A.   Variances of generations for component first bloom

| Statistics | Block no. | | | | | Expected | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Pooled | Inc. | Exc. |
| $V_{F2}$ | 8.73 | 11.78 | 11.38 | 13.00 | 11.22 | 10.25 | 10.48 |
| $V_{\overline{F3}}$ | 11.53 | 12.69 | 7.66 | 12.32 | 11.05 | 9.57 | 9.57 |
| $V_{F2/F3}$ | 5.41 | 5.37 | 4.31 | 5.55 | 5.16 | 7.38 | 7.38 |
| $\overline{V}_{F3}$ | 6.17 | 6.10 | 5.83 | 6.33 | 6.11 | 6.57 | 6.11 |
| $E_1$ | 2.36 | 2.53 | 2.41 | 2.26 | 2.39 | 2.90 | 3.13 |
| $E_2$ | 1.14 | .54 | .41 | .62 | .68 | 2.16 | 2.16 |

Inc.   Inclusive of $\overline{V}_{F3}$

Exc.   Exclusive of $\overline{V}_{F3}$, given perfect fit.


Table 18B.        Analysis of variance

| Source | D.F. | S.S. | F | |
|---|---|---|---|---|
| Total | 20 | 70.1353 | | |
| Linkage | 1 | 1.2834 | .85 | n.s. |
| Interaction | 1 | 41.6620 | 27.58 | p < .005 |
| Error | 18 | 27.1899 | | |

n.s.  not significant at chosen alpha = .05


Table 18C.        Estimates of parameters

| | | |
|---|---|---|
| D | 14.85 | $\pm$ 1.99 |
| H | -.30 | $\pm$ 6.38 |
| $E_1$ | 2.90 | $\pm$ 0.54 |
| $E_2$ | 2.16 | $\pm$ 0.55 |

Table 19A. Variances of generations for component fruit set

| Statistics | Block no. | | | | | Expected | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Pooled | Inc. | Exc. |
| $V_{F2}$ | 1.04 | 1.11 | 1.05 | 1.04 | 1.06 | 1.01 | 1.02 |
| $V_{\overline{F3}}$ | .46 | .38 | .23 | .28 | .34 | .27 | .27 |
| $W_{F2/F3}$ | .12 | .08 | .05 | .09 | .09 | .19 | .19 |
| $\overline{V}_{F3}$ | .88 | .68 | .66 | .74 | .74 | .77 | .74 |
| $E_1$ | .49 | .49 | .49 | .56 | .51 | .53 | .54 |
| $E_2$ | .15 | .08 | .18 | .19 | .15 | .22 | .22 |

Table 19B. Analysis of variance

| Source | D.F. | S.S. | F | |
|---|---|---|---|---|
| Total | 20 | .1799 | | |
| Linkage | 1 | .0052 | 1.19 | n.s. |
| Interaction | 1 | .0955 | 21.67 | $p < .005$ |
| Error | 18 | .0793 | | |

Table 19C. Estimates of parameters

| | | |
|---|---|---|
| D | $-.20 \pm 0.11$ | |
| H | $2.32 \pm 0.34$ | |
| $E_1$ | $.53 \pm 0.03$ | |
| $E_2$ | $.22 \pm 0.03$ | |

Table 20A.　Variances of generations for component ripe fruit

| Statistics | Block no. | | | | | Expected | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Pooled | Inc. | Exc. |
| $V_{F2}$ | 11.17 | 14.03 | 8.64 | 11.77 | 11.40 | 9.74 | 9.60 |
| $V_{\overline{F3}}$ | 25.42 | 19.08 | 28.34 | 20.71 | 23.39 | 19.79 | 19.79 |
| $W_{F2/F3}$ | 4.51 | 4.62 | 4.09 | 4.08 | 4.33 | 9.72 | 9.72 |
| $\overline{V}_{F3}$ | 9.36 | 8.67 | 9.29 | 8.81 | 9.03 | 8.75 | 9.03 |
| $E_1$ | 6.06 | 5.19 | 3.78 | 8.26 | 5.82 | 7.76 | 7.62 |
| $E_2$ | 1.93 | 1.12 | 1.51 | 5.88 | 2.61 | 6.21 | 6.21 |

Table 20B.　Analysis of variance

| Source | D.F. | S.S. | F | |
|---|---|---|---|---|
| Total | 20 | 340.9690 | | |
| Linkage | 1 | .7600 | .14 | n.s. |
| Interaction | 1 | 245.3534 | 46.57 | $p < .005$ |
| Error | 18 | 94.8450 | | |

Table 20C.　Estimates of parameters

| | | |
|---|---|---|
| D | $34.91 \pm 3.72$ |
| H | $-68.88 \pm 11.92$ |
| $E_1$ | $7.76 \pm 1.01$ |
| $E_2$ | $6.21 \pm 1.02$ |

the squared deviations from the pooled estimates. A residual variance due to genic interaction is found as the difference between the total variance and the summed linkage and error variances.

There remains the assignment of degrees of freedom to complete the analysis of variance format. Since four values are observed for each of six equations there is a total of 24 degrees of freedom. Four degrees of freedom are used up by the estimates D, H, $E_1$, and $E_2$. Each equation contributes 3 degrees of freedom for error leaving from the total 2 degrees of freedom, one each for linkage and residual genic interactions.

## The components of maturity

The measurement of the components of maturity are similar to those described for the first two experiments. In the analysis of the component ripe fruit, precautions are taken to relate all measurements to the first position of the first inflorescence. All ripe fruits not in this location are corrected by regression to the standard position. Various estimates of the regression coefficient are presented in table 21, and it is concluded that they are not all of the same population of $\beta$. Corrections, therefore, are made from the explicit b calculated for each generation, and in the case of $F_3$ families, for each family separately.

It is clear from the significant interaction (tables 18B, 19B, and 20B) displayed for each component that the arithmetic scale does not make the loci additive. The interaction may be of a genetic nature as well as of an environmental cause, but most reasonably due to both. Were it strictly a genotype-environment interaction, it would be detected in the instability of the standard errors of parents and $F_1$'s (table 16). To the contrary, there is stability and no obvious

Table 21A.    Regression analysis of component ripe fruit on position

| Source | D.F. | S.S. | F | |
|--------|------|------|---|---|
| Total | 2799 | 140922 | | |
| Regression | 1 | 21658 | 508 | p < .005 |
| Residual | 2798 | 119264 | | |

Table 21B.        Estimates of $\beta$

| | |
|---|---|
| General | 15.63 |
| Block no. 1 | 10.15 |
| no. 2 | 15.98 |
| no. 3 | 16.58 |
| no. 4 | 15.22 |
| Generation | |
| Red Currant | 9.33 |
| Tangerine | 6.56 |
| $F_1$ | 7.48 |
| $F_2$ | 6.38 |
| $F_3$ | 16.49 |
| Range in $F_3$ families | |
| From | -6.27 |
| To | 21.84 |

95% Confidence Interval

$$14.27 < \beta < 16.99$$

mean-variance correlation. Therefore, at least some of the interaction must be of an epistatic nature. In any case, as interaction is basic to the interpretation of the estimates D and H (tables 18C, 19C, and 20C) it will be desirable to examine its nature.

Hayman and Mather (1955) showed how estimates of D and H were affected by inter-loci modifications. We have already seen, for example, that the variance of the $F_2$ involves the components $1/2$ D + $1/4$ H where D = $\Sigma(d^2)$ and H = $\Sigma(h^2)$. With epistasis, $V_{F2}$ = $1/2\ d_\alpha^2$ + $1/2\ d_\beta^2$ + $1/4\ h_\alpha^2$ + $1/4\ h_\beta^2$ + $1/4\ i_{\alpha\beta}^2$ + $1/8\ j_{\alpha/\beta}^2$ + $1/8\ j_{\beta/\alpha}^2$ + $1/16\ 1_{\alpha\beta}^2$. That is, in a digenic system where loci $\alpha$ and $\beta$ interact, the estimates D and H are inflated by the interaction terms i, j, and l. While the interaction term j is correlated with d in $\overline{V}_{F3}$, $V_{\overline{F3}}$, and $W_{F2/F3}$, the interaction term l is associated with h. In the $\overline{V}_{F3}$ and $V_{\overline{F3}}$, the parameter D takes the form $\Sigma(d_\alpha - 1/4\Sigma j_{\alpha/\beta})^2$ and H = $\Sigma(h_\alpha - 1/4\Sigma 1_{\alpha\beta})^2$. Likewise in $W_{F2/F3}$ D = $\Sigma d_\alpha(d_\alpha - 1/4\Sigma j_{\alpha/\beta})$ and H = $\Sigma h_\alpha(h_\alpha - 1/4\Sigma 1_{\alpha\beta})$.

Keeping this in mind we find in tables 18C, 19C, and 20C that the parameters D and H are not always reliable. A negative value is unreasonable for a parameter based on squared observations. Parameter D for the components first bloom and ripe fruit appear reasonable as does H for fruit set. The others must be grossly underestimated. A large epistatic term of the nature of $j_{\alpha/\beta}$ (homozygous and heterozygous loci interaction) could explain in part the low D value of fruit set. Likewise, large epistatic terms of the nature of $1_{\alpha\beta}$ (heterozygous and heterozygous loci) could explain the low H value of the components first bloom and ripe fruit.

## Model of generation means

The Hayman and Mather (1955) model using generation means can be summarized as follows:

$$\overline{P}_1 = +d_\alpha +d_\beta +i_{\alpha\beta}/ - 1/2\, j_{\alpha/\beta} - 1/2\, j_{\beta/\alpha} + 1/4\, l_{/\alpha\beta}$$

$$\overline{P}_2 = -d_\alpha -d_\beta +i_{\alpha\beta}/ + 1/2\, j_{\alpha/\beta} + 1/2\, j_{\beta/\alpha} + 1/4\, l_{/\alpha\beta}$$

$$\overline{F}_1 = h_\alpha +h_\beta + 1/4\, l_{/\alpha\beta}$$

$$\overline{F}_2 = 1/2\, [h_\alpha +h_B]$$

$$\overline{F}_3 = 1/4\, [h_\alpha +h_\beta + 1/4\, l_{/\alpha\beta}]$$

If the alleles affecting the character in the same direction are dispersed rather than associated the reading for every other sign in the parents should be reversed. This model was generalized and simplified by Hayman (1958) by adding to the equation for each generation the statistic m which stands for the generalized mean over all generations. Then by using the $\overline{F}_2$ as the standard or pivotal generation and reducing all other generations by its equation a relatively simple and general model results:

$$\overline{P}_1 = m + d - 1/2\, h + i - j + 1/4\, l$$

$$\overline{P}_2 = m - d - 1/2\, h + i + j + 1/4\, l$$

$$\overline{F}_1 = m + 1/2\, h \qquad\quad + 1/4\, l$$

$$\overline{F}_2 = m$$

$$\overline{F}_3 = m - 1/4\, h \qquad\quad + 1/16\, l$$

To solve for the six unknowns, backcross generations would have to be included in the experiment to provide at least as many equations as unknowns. In the example of generation equations presented d and j are confounded and can be obtained as one unknown d'. Hayman feels that

because of this model's flexibility and simplicity it is the most reliable devised to date.

The means found in table 16 are substituted in these equations and solved by the same methods used in the variance models. The results are presented in table 22. The interaction of the l-type suspected in the variance models for first bloom and ripe fruit are substantiated in this model. The j-type interaction suspected in fruit set cannot be detected because of the lack of backcross generations.

The results of the two types of models, that of variances and that of generation means, are in good agreement. In the component first bloom 48% of the gene action is additive, 12% is due to dominance and 40% is interaction. In the component ripe fruit 33% is additive, 30% dominance and 37% interaction (table 22). Interaction contributes as much to the variation between generations as does the additive portion. Fruit set cannot be evaluated because the extent of its interaction is not known. It would be desirable to have values for the j-type interaction in the components first bloom and ripe fruit, if only to complete the analysis.

Correlation coefficients were calculated for the three pairs of components (see table 23). Genetically the components first bloom and fruit set are related as well as components first bloom and ripe fruit. However, components fruit set and ripe fruit do not appear to be. The methods used for extracting the environmental influence were not the most critical and there may be some residual influence confounded with the genetic correlation coefficients. Comparison of the $r_p$ and $r_g$ for the $F_2$ suggests this in part. The differing nature of the interactions

Table 22.  Means of generations, theoretical values, and calculated parameters from the linear model

| Generations | Theoretical values | Estimates of the parameters |
|---|---|---|
| **Component first bloom** | | |
| $P_E$  51.90 $\pm$ .11 | 51.90 | m  54.38 $\pm$ .18 |
| $P_L$  59.31 $\pm$ .10 | 59.32 | d'  3.71 $\pm$ .15 |
| $F_1$  54.65 $\pm$ .18 | 54.66 | h  - .93 $\pm$ .38 |
| $F_2$  54.40 $\pm$ .14 | 54.38 | i  .02 $\pm$ .30 |
| $F_3$  54.77 $\pm$ .10 | 54.80 | l  2.99 $\pm$ 1.17 |
| **Component fruit set** | | |
| $P_E$  3.50 $\pm$ .05 | 3.49 | m  3.18 $\pm$ .08 |
| $P_L$  4.04 $\pm$ .06 | 4.03 | d'  .27 $\pm$ .06 |
| $F_1$  3.10 $\pm$ .06 | 3.11 | h  -.60 $\pm$ .16 |
| $F_2$  3.26 $\pm$ .04 | 3.18 | i  .05 $\pm$ .13 |
| $F_3$  3.30 $\pm$ .02 | 3.39 | l  .93 $\pm$ .50 |
| **Component ripe fruit** | | |
| $P_E$  37.18 $\pm$ .16 | 37.17 | m  39.79 $\pm$ .41 |
| $P_L$  56.82 $\pm$ .24 | 56.81 | d'  9.82 $\pm$ .34 |
| $F_1$  38.09 $\pm$ .19 | 38.10 | h  -8.80 $\pm$ .87 |
| $F_2$  39.85 $\pm$ .15 | 39.79 | i  .09 $\pm$ .69 |
| $F_3$  42.56 $\pm$ .14 | 42.67 | l  10.82 $\pm$ 2.72 |

for the components may also account for some of the reasons fruit set and ripe fruit are not significantly correlated. Taking the $r_g$ to be reliable would indicate that first bloom and fruit set have genes in common, but with opposing effects. First bloom and ripe fruit also have genes in common with similar effects. Fruit set and ripe fruit leave no common genes to be detected. The results are not unreasonable, but neither are they very reliable.

Table 23. Correlations between components of maturity.

| Generation | | Pairs of Components | | |
| | | First bloom fruit set | First bloom ripe fruit | Fruit set ripe fruit |
|---|---|---|---|---|
| Red Currant | $r_p$ | -.63* | -.12* | -.06 |
| Tangerine | $r_p$ | +.00 | -.17* | -.07 |
| $F_1$ | $r_p$ | -.52* | -.42* | +.11 |
| $F_2$ | $r_p$ | -.60* | +.00 | -.04 |
| $F_2$ | $r_g$ | -.83* | +.12* | -.04 |

\* significant beyond chosen alpha = .05

$r_p$ phenotypic coefficient of correlation

$r_g$ genetic coefficient of correlation

## DISCUSSION

Three experimental units have been devised to study the inheritance of maturity in tomato species. The first utilizes gene markers, especially of chromosome 2, to locate the effects of maturity in the tomato genome. In the second unit, a range of varieties selected by their total expression of maturity make it possible to study the components' ordinal relationships. The third unit provides estimates of various genetical parameters and is therefore, primarily statistical.

Only the components first bloom and ripe fruit will be discussed here, two reasons being, 1) that together, first bloom and ripe fruit account for 96% of the total difference between the earliest and the latest of the varieties used in these experiments, and 2) the $F_2$ distribution of fruit set has only 6 classes in the original data, too few for a critical analysis. The $F_2$ distributions of the components to be discussed have at least 20 classes.

Both first bloom and ripe fruit had their major influence under the control of the second chromosome. The effects in each case can be attributed to two regions, or genes as it were, of unequal strength. On the average one region is twice as influential as the other (figure 2). These components, in the second experiment, consist of parent varieties grouping into four classes. The ordinal rank of the varieties in each class are not similar for the two components, nor are the constituents the same (table 9). This poses the question of whether first bloom and ripe fruit are, in a strict sense, controlled by the same genes or that they do in fact differ in degree if not in total.

- 68 -

Testing the integrity of a "two regions-two genes" hypothesis supported by the first experiment should clarify to what extent the two components are similar. With two rigid loci, nine possible genotypes exist. Given that $d_\alpha = 2d_\beta$ and $h_\alpha = 2h_\beta$ it is possible to construct the theoretical values for each of the nine genotypes. For the components first bloom and ripe fruit these are as follows, with the aid of d, h, i, and l of table 22:

|  | AA $-d_\alpha$ | Aa $h_\alpha$ | aa $+d_\alpha$ |  |
|---|---|---|---|---|
| BB | 51.90 days | 52.23 days | 56.80 days | First bloom |
| $-d_\beta$ | 37.17 days | 32.34 days | 50.09 days | Ripe fruit |
| Bb | 51.31 days | 54.66 days | 56.25 days | First bloom |
| $h_\beta$ | 32.00 days | 38.10 days | 45.10 days | Ripe fruit |
| bb | 54.34 days | 54.71 days | 59.32 days | First bloom |
| $+d_\beta$ | 43.53 days | 38.88 days | 56.81 days | Ripe fruit |

The values for AABB, AaBb, and aabb are those derived theoretically for $P_E$, $F_1$, and $P_L$, respectively, as presented in the section on a model using generation means. The formulae for calculating the values of AABB, AaBb, aabb, as well as the remaining six genotypes, are derived in a set of linear comparisons similar to methods employed in the analysis of variance (Hayman and Mather, 1955).

Certain heterozygotes express a value outside the range of the parents (as denoted by the genotypes AABB and aabb). Tables 11 to 15 show such manifestations of hybrid vigor. Burdick (1954) reported similar findings.

In a digenic cross as presented above the $F_2$ consists of the

genotypic ratio: 1AABB : 2AABb : 1AAbb : 2AaBB : 4AaBb : 2Aabb : 1 aaBB : 2aaBb : 1 aabb with independent segregation of the two loci. In the case of experiment one the two regions of the second chromosome are sufficiently far apart to be assumed independent of linkage. Further, linkage escaped detection in the analysis of the variance models in experiment three. It is possible to construct a theoretical $F_2$ distribution for comparison with that observed.

Powers, Locke, and Garrett (1950) showed that a theoretical distribution can be constructed including environmental effects as error variance. Certain intervals are chosen and the observed data grouped. If more than one theoretical generation is constructed to compare with various observed ones the interval sizes must be consistent throughout. By calculating the absolute difference between the lower boundary of the interval and the mean of a given genotype, divided by its standard deviation gives a value x for that interval. The value x is transformed into a theoretical frequency by the use of a table with areas of the normal distribution given in terms of standard deviations. Each genotype then gives a set of frequencies and are combined in the ratio expected for that generation. The standard deviations for AABB, AaBb, and aabb are those observed for the parents and $F_1$. By regression methods (Powers, 1942) a standard deviation is calculated for each genotype.

The $F_2$ distribution of the component first bloom and its expected distribution can be grouped as follows, marking intervals with the lower boundary:

| days | 45 | 48 | 51 | 54 | 57 | 60 | totals |
|---|---|---|---|---|---|---|---|
| observed frequencies | 16 | 66 | 131 | 184 | 130 | 33 | 560 plants |
| theoretical frequencies | 6 | 56 | 196 | 218 | 73 | 11 | 560 plants |

A test for the goodness of fit reveals a $Chi^2$ of 133.8 for 5 degrees of freedom. The observed do not fit the theoretical. Either the data do not support the hypothesis of $d_\alpha = 2d_\beta$ or that d' contains a significant j-type interaction with which d is confounded.

A j-type interaction is described as the non-additive effect due to a heterozygous locus with a homozygous locus. It is the sum of the type $j_{\alpha/\beta}$ and $j_{\beta/\alpha}$ for which no separation will be attempted here. A j-type interaction is demonstrated in the first experiment for the component first bloom (table 7). According to Hayman (1958) d' = d - j in the late parent and d' = -d + j in the early parent. Arbitrarily setting j at 1.50 (half way between i and 1 of table 22) $d_\alpha$ becomes 3.47, $d_\beta$ = 1.74, $h_\alpha$ = -.62, $h_\beta$ = -.31, i = .02, and 1 = 2.99, where d = 5.21. The values for the genotypes become:

|  | AA | Aa | aa |
|---|---|---|---|
| BB | 51.90 | 50.98 | 57.30 |
| Bb | 49.56 | 54.66 | 58.00 |
| bb | 53.84 | 55.96 | 59.32 |

and the distributions:

| days | 45 | 48 | 51 | 54 | 57 | 60 | totals |
|---|---|---|---|---|---|---|---|
| observed frequencies | 16 | 66 | 131 | 184 | 130 | 33 | 560 plants |
| theoretical frequencies | 13 | 93 | 141 | 176 | 112 | 25 | 560 plants |

This gives a $Chi^2$ = 10.3 which has a probability of greater than .05 with 5 d.f. If in fact j = 1.50 then the hypothesis of $d_\alpha = 2d_\beta$ supported by the first experiment for the component first bloom is also reasonable in the third experiment. A significant j-type interaction is supported

by the first experiment for first bloom (table 7).

The soundness of the proposed model can be further examined by reducing the total observed distribution to the block distributions and testing for heterogeneity.

| class | | 45 | 48 | 51 | 54 | 57 | 60 | d.f. | Chi$^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|
| block no. | 1 | 3 | 14 | 33 | 51 | 34 | 8 | 4 | 8.4 | >.05 |
| | 2 | 7 | 21 | 37 | 42 | 32 | 5 | 4 | 2.0 | >.50 |
| | 3 | 3 | 19 | 35 | 44 | 35 | 10 | 4 | 6.3 | >.10 |
| | 4 | 3 | 28 | 26 | 47 | 29 | 10 | 4 | 5.3 | >.25 |
| totals | | | | | | | | 16 | 22.0 | |
| combined | | 16 | 66 | 131 | 184 | ·130 | 33 | 5 | 10.3 | >.05 |
| heterogeneity | | | | | | | | 11 | 11.7 | >.25 |
| mean dist. | | 4 | 17 | 33 | 46 | 32 | 8 | 4 | 2.3 | >.50 |

No heterogeneity of significance can be detected and a good fit is observed between the theoretical and actual distributions.

The component ripe fruit has an observed $F_2$ distribution, in intervals of 4 days as follows:

| days | 31 | 35 | 39 | 43 | 47 | 51 | 55 | total |
|---|---|---|---|---|---|---|---|---|
| observed | 42 | 190 | 238 | 66 | 17 | 6 | 1 | 560 plants |

No attempt was made to fit the observed to a theoretical distribution. The late parent representing the genotype aabb has a mean value of 56.8 days. In an $F_2$ population of 560 plants 35 plants should group about the value 57. Only one such plant was observed. A theoretical distribution based on $d_\alpha = 2d_\beta$ would have far too many plants for the interval 55+ days. Interaction of the sort postulated for first bloom is ruled out here since i is the only type of interaction which could effect aabb, and i is not significant (table 22). Under most simple models at least 5 independent genes are needed to explain the results above. Since in terms of quantitative genetics 30 crossover units between loci cannot be

detected easily, 5 loci on one chromosome showing independence would imply a length of at least 120 map units. Moens and Butler (1963) have reported that about 28 crossover units separated compound inflorescence with the centromere. This would place mottled and dwarf about 80 map units from the centromere and at least two regions of influence on maturity are detected within the range of the markers. It would appear that a two gene model would be of limited use in relation to ripe fruit.

In a model of 5 independent loci, one observation in 1,024 should have the genotype aabbccddee. With 4 independent loci, one observation in 256 should have the genotype aabbccdd. One plant in 560 of the $F_2$ is reported to be similar to the late parent, placing the observed value between the 4 and 5 loci models. It is noted, however, that the observed value of 57 days is somewhat removed from the remainder of the distribution, the next closest being under 55 days. This favors the 5 gene hypothesis. With reliable estimates of D and H it is possible according to Mather (1949) to estimate the number of genes (k) involved in differentiating the parents by the formulae $k_1 = \Sigma^2 d/\Sigma d^2$ and $k_2 = \overline{V}_{F3}/V_{VF3}$. Adjusting the obtained D and H of table 20C in view of the interaction obtained in the model of generation means (table 22), a five gene model appeared reasonable.

Before devising a model using the parameters d', h, i, and l of table 22 some attempt should be made to extract j from d'. Under complete dominance d and j are similar (figure 1) and as d' = 9.82, h = -8.80, j must inflate d by about -1.00 (table 22). A 5 gene model is constructed from the parameters d = 8.82, h = -8.80, i = .09, j = -1.00, and l = 10.82.

Though there is no support for a significant j-type interaction (tables
7, 20, and 22) it becomes theoretically important as it contributes,
as does the non-significant i interaction, to the pattern of the distribu-
tion. The calculated genotypes take the following frequencies and
values in the $F_2$:

| | | | |
|---|---|---|---|
| 1 | AABBCCDDEE | 37.17 days | |
| 10 | AABBCCDDEe | 35.57 " | |
| 40 | AABBCCDdEe | 34.86 " | |
| 80 | AABBCcDdEe | 35.05 " | |
| 80 | AABbCcDdEe | 36.13 " | |
| 32 | AaBbCcDdEe | 38.10 " | |
| 5 | AABBCCDDee | 41.22 " | |
| 40 | AABBCCDdee | 39.24 " | |
| 120 | AABBCcDdee | 38.36 " | |
| 160 | AABbCcDdee | 38.36 " | |
| 80 | AaBbCcDdee | 39.26 " | |
| 10 | AABBCCddee | 44.91 " | |
| 60 | AABBCcddee | 42.95 days |
| 120 | AABbCcddee | 41.88 " |
| 80 | AaBbCcddee | 41.71 " |
| 10 | AABBccddee | 48.84 " |
| 40 | AABbccddee | 46.60 " |
| 40 | AaBbccddee | 45.45 " |
| 5 | AAbbccddee | 52.80 " |
| 10 | Aabbccddee | 50.48 " |
| 1 | aabbccddee | 56.81 " |

1024

$\overline{F}_2 = 39.79$ days (theoretical)

The genotypes are representative of classes and no higher than second
degree interactions are incorporated into the calculations.

Following the method outlined the theoretical distribution is as
follows:

| days | 31 | 35 | 39 | 43 | 47 | 51 | 55 | totals |
|---|---|---|---|---|---|---|---|---|
| observed | 42 | 190 | 238 | 66 | 17 | 6 | 1 | 560 plants |
| theoretical | 63 | 199 | 184 | 81 | 25 | 8 | 0 | 560 plants |

The test for goodness of fit gives a $\text{Chi}^2$ of 28.7 with 5 d.f. It appears
the model is not supported by the observed data. Testing for heterogeneity,

| class | | 31 | 35 | 39 | 43 | 47 | 51 | d.f. | $\text{Chi}^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|
| block no. | 1 | 4 | 43 | 61 | 25 | 6 | 1 | 3 | 11.7 | < .010 |
| | 2 | 8 | 49 | 57 | 17 | 7 | 2 | 4 | 7.3 | > .100 |
| | 3 | 14 | 58 | 53 | 13 | 1 | 1 | 3 | 8.6 | < .050 |
| | 4 | 16 | 40 | 67 | 11 | 3 | 3 | 4 | 16.1 | < .005 |
| totals | | | | | | | | 14 | 43.7 | < .005 |
| mean dist. | | 11 | 47 | 59 | 17 | 4 | 2 | 4 | 6.3 | > .100 |

large discrepancies are exhibited between blocks. The model fits the
mean of the block distributions and this is reasonable as all calculations
are based on means, but the total Chi$^2$ of 43.7 with 14 d.f. would
indicate that one model could not fit all four blocks. It is suspected
that the differences exhibited between blocks reflects differences in
the soil and that under the circumstances the model presented provides
the best indication of actual gene action possible. In addition,
interactions cannot be regarded as wholly genetic but also of a genotype-
environmental nature.

The "two regions-two genes" postulate is useful, nevertheless,
when used in conjunction with experiment two. In table 9 examples are
cited of varieties in which the level of gene activity for maturity is
fixed. These may be classed into clearly distinct groups. It is only
with segregating generations in ripe fruit that the effects of the regions
are being split up to weaken or destroy the two loci postulate. This
can often be expected. What is defined for convenience in one instance
is not necessarily useful in another. While it is justified it helps to
make the way clear into the analysis of other aspects under examination.

Powers, Locke, and Garrett (1950) provide the only work in
tomatoes with which the results of the third experiment can be compared.
They attributed 3 major gene pairs differentiating the parents in the
component first bloom, 2 in the component ripe fruit, and 8 from seeding
to ripe fruit. They recognized that interaction was at work but could
only speculate on what genotypes it was expressed. They depended on
means for estimates of the number of gene pairs operating and based the
premises of interaction on the lack of conformity between expected and

observed. The method involves manipulations and adjustments of the genotypes until finally the differences between actual and theoretical are no longer significant. That the interactions presented are not reliable does not invalidate their report. Discrepancies other than interaction appear in their report from the work presented here. What appears to be an underestimate of gene pairs differentiating parents in the components is due mostly to the degree of contrast between their parents and those presented here. In the component first bloom only 12 days differentiated the parents Porter and Ponderosa, while 14 days separated the parents in ripe fruit. The component fruit set had limits defined differently in that the fruit was noted set only after size changes in the ovary were obvious. The means of the two parents were 6.9 days and 37.5 days. In total the parents differed by 57 days and fruit set accounted for 54% of total maturity time compared to 45% here. Many of the results for fruit set were vague in this presentation. Powers, et. al. (1950) found this to be so with their component and incorporated it with ripe fruit. The climatic conditions under which the two experiments were grown were vastly different.

# CONCLUSIONS

The genetic analysis of maturity in terms of earliness was studied in three major components, 1) seeding to first bloom, 2) first bloom to fruit set, and 3) fruit set to ripe fruit. Constant parent regression techniques, variance models and linear models were used to analyze the data. From them it was concluded that:

1) Maturity is inherited, and as much as 48% of the variation between generations is additive in the component first bloom, and 33% in ripe fruit.

2) Dominance of the earliness phase is general for all components; complete in the components fruit set and ripe fruit, partial in first bloom.

3) Interaction in the form of epistasis prevails in all components. It accounts for 40% of the variation in first bloom, and 37% in ripe fruit. Heterozygous locus and homozygous locus epistasis as well as heterozygous-heterozygous type epistasis was detected in the component first bloom. Only heterozygous-heterozygous type epistasis was demonstrated for ripe fruit. A predominantly heterozygous-homozygous type was suggested for fruit set. The remaining type, homozygous-homozygous, was clearly absent in all phases of experimentation.

4) Two loosely defined regions of chromosome 2 genetically regulate the manifestation of maturity in all components. However, in the $F_2$ distributions two gene pairs, $\alpha = 1/2 \ \beta$, explain the observations in first bloom, while at least 5 gene pairs are needed to account for that

- 77 -

of the ripe fruit. The region "mottled-dwarf" of chromosome 2 accounts for an influence of -4 days in first bloom, -.5 days in fruit set, -14 days in ripe fruit. The "compound inflorescence" region accounted for -1 to +4 days at first bloom, -.5 days at fruit set, and -7 days at ripe fruit.

5) The components showed that the genetics of maturity is not constant in time.

## LITERATURE CITED

Anderson, V. L. and Kempthorne, O. 1954. A model for the study of quantitative inheritance. _Genetics_ 39: 883-898.

Breese, E. L. and Mather, K. 1957. The organization of polygenic activity within a chromosome in _Drosophila_. I. Hair characters. _Heredity_ 11: 373-395.

_____. 1960. The organization of polygenic activity within a chromosome in Drosophila. II. Viability. _Heredity_ 14: 375-399.

Burdick, A. B. 1949. Heterosis in the tomato: estimation of the relative contribution of epistasis and dominance. Unpub. Ph.D. thesis, University of California, Berkeley.

_____. 1954. Genetics of heterosis for earliness in the tomato. _Genetics_ 39: 488-505.

Butler, L. 1941. Inheritance of fruit size in the tomato. _Can. J. Res._ C, 19: 216-224.

_____. 1960. The linkage map of chromosome 2 of the tomato. _Can. J. Bot._ 38: 365-379.

Cavalli, L. L. 1952. An analysis of linkage in quantitative inheritance. _Quantitative Inheritance_, H. M. S. O., London, pp. 135-144.

Clayton, G. A., Knight, G. R., Morris, J. A. and Robertson, A. 1957. An experimental check on quantitative genetical theory. I. Short term responses to selection. _J. Genet._ 55: 131-151.

Cockerham, C. C. 1954. An extension of the concept of partitioning hereditary variance for analysis of covariances among relatives when epistasis is present. _Genetics_ 39: 859-882.

_____. 1956. Effects of linkage on the covariances between relatives. _Genetics_ 41: 138-141.

_____. 1957. Analysis of quantitative gene action. _Brookhaven Symp. in Biol._ Genetics in Plant Breeding. No. 9 pp. 53-68.

Currence, T. M. 1932. Genetic association between qualitative and quantitative characters in the tomato. _Proc. Sixth Intern. Congress Genetics_ 2: 32-34.

Currence, T. I:. 1938. The relation of the first chromosome pair to date of fruit ripening in the tomato (Lycopersicon esculentum). Genetics 23: 1-11.

Falconer, D. S. 1961. Introduction to Quantitative Genetics, Oliver and Boyd, Edinburgh, pp. 365 + x.

Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. Trans. Roy. Soc. Edin. 52: 399-433.

_____, Immer, F. R. and Tedin, O. 1932. The genetical interpretation of statistics of the third degree in the study of quantitative inheritance. Genetics 17: 107-124.

Gilbert, N. 1960. Quantitative inheritance in Drosophila. J. Genet. 57(1): 77-83.

Griffing, B. 1948. Statistical analysis of gene action in components of tomato yield. Unpub. Ph.D. thesis, Iowa State College, Ames.

_____. 1950. Analysis of quantitative gene action by constant parent regression and related techniques. Genetics 35: 303-321.

_____. 1953. An analysis of tomato yield components in terms of genotypic and environmental effects. Iowa Agr. Expt. Research Bull. 397: 324-380.

_____. 1954. Contributions of genotypic and environmental effects to earliness of tomato fruiting. Statistics and Mathematics in Biology, Iowa State College Press, Ames.

Groth, B. H. A. 1914. The "Golden Mean" in the inheritance of size. Science 39: 581-584.

_____. 1915. Inheritance of fruit size in Lycopersicon. New Jersey Agr. Expt. Sta. Bull. 278.

Hayman, I. 1954. The theory and analysis of diallel crosses. Genetics 6: 789-809.

_____. 1957. Interaction, heterosis and diallel crosses. Genetics 42: 336-355.

_____. 1958. The separation of epistatic from additive and dominance variation in generation means. Heredity 12: 371-390.

_____ and Mather, K. 1955. The description of genic interactions in continuous variation. Biometrics 11: 69-82.

Horner, T. W., Comstock, R. E. and Robinson, H. F. 1955. Non-allelic gene interactions and the interpretation of quantitative genetic data. Tech. Bull. N. C. Agric. Exp. Sta. No. 118 pp. 117 + v.

Johannsen, W. 1903. Heredity in populations and pure lines. Classic Papers in Genetics, Prentice-Hall, Englewood Cliffs, N. J. pp. 20 to 26.

Kempthorne, O. 1955. As part of the discussion on Hayman's presentation. The description and analysis of gene action and interaction. Cold Spr. Harb. Symp. quant. Biol. 20: 84-86.
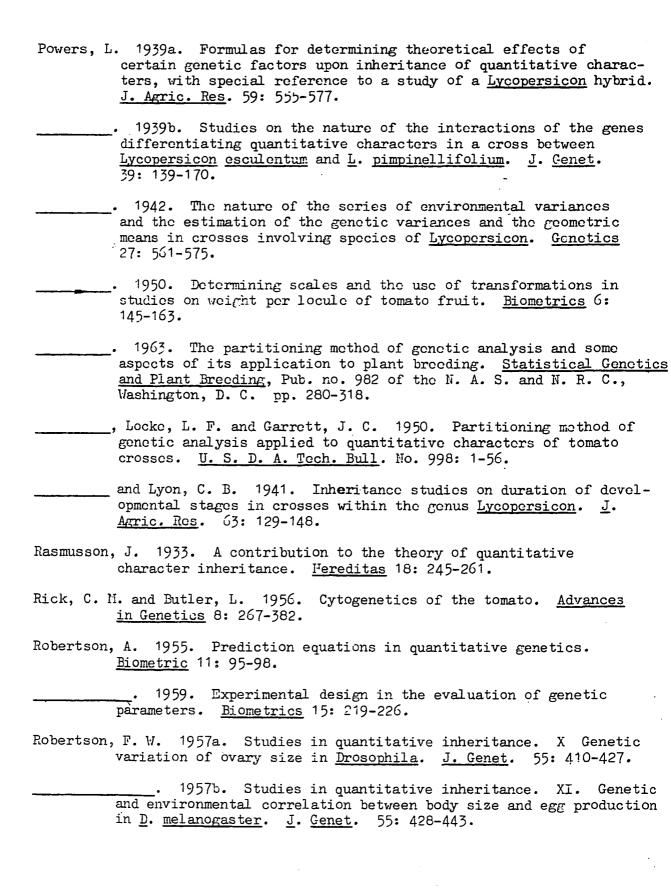
_____. 1957. An Introduction to Genetic Statistics, Wiley, New York, pp. 545 + xviii.

Kheiralla, A. I. and Whittington, W. J. 1962. Genetic analysis of growth in tomato: for $F_1$ generation. Ann. Bot. (London) 26(104): 489-504.

Leonard, W. H., Mann, H. O. and Powers, L. 1957. Partitioning method of genetic analysis applied to plant height inheritance in barley. Colorado Agr. Exp. Sta. Tech. Bull. 60: 24 pp.

Lerner, I. M. 1950. Population Genetics and Animal Improvement, Cambridge University Press, Cambridge, pp. 342 + xviii.

MacArthur, J. W. 1941. Size inheritance in tomato fruits. J. Hered. 32: 291-295.

_____. and Butler, L. 1938. Size inheritance and geometric growth processes in the tomato fruit. Genetics 23: 253-268.

Mather, K. 1949. Biometrical Genetics, Methuen, London, pp. 162 + x.

Moens, P. and Butler, L. 1963. The genetic location of the centromere of chromosome no. 2 in the tomato (Lycopersicon esculentum). Can. J. Genet. Cytol. 5: 364-370.

Mohamed, A. H. and Hanna, A. S. 1964. Inheritance of quantitative characters in rice. I. Estimation of the number of effective factor pairs controlling plant height. Genetics 49: 81-93.

Myers, C. E. 1924. Statistical studies of inheritance in the tomato. Penn. State Coll. Agr. Exp. Sta. Bull. 189: 31 pp.

Panse, V. G. 1940. Application of genetics to plant breeding. II. The inheritance of quantitative characters and plant breeding. J. Genet. 40: 283-302.

Powers, L. 1939a. Formulas for determining theoretical effects of certain genetic factors upon inheritance of quantitative characters, with special reference to a study of a Lycopersicon hybrid. J. Agric. Res. 59: 555-577.

_____. 1939b. Studies on the nature of the interactions of the genes differentiating quantitative characters in a cross between Lycopersicon esculentum and L. pimpinellifolium. J. Genet. 39: 139-170.

_____. 1942. The nature of the series of environmental variances and the estimation of the genetic variances and the geometric means in crosses involving species of Lycopersicon. Genetics 27: 561-575.

_____. 1950. Determining scales and the use of transformations in studies on weight per locule of tomato fruit. Biometrics 6: 145-163.

_____. 1963. The partitioning method of genetic analysis and some aspects of its application to plant breeding. Statistical Genetics and Plant Breeding, Pub. no. 982 of the N. A. S. and N. R. C., Washington, D. C. pp. 280-318.

_____, Locke, L. F. and Garrett, J. C. 1950. Partitioning method of genetic analysis applied to quantitative characters of tomato crosses. U. S. D. A. Tech. Bull. No. 998: 1-56.

_____ and Lyon, C. B. 1941. Inheritance studies on duration of developmental stages in crosses within the genus Lycopersicon. J. Agric. Res. 63: 129-148.

Rasmusson, J. 1933. A contribution to the theory of quantitative character inheritance. Hereditas 18: 245-261.

Rick, C. M. and Butler, L. 1956. Cytogenetics of the tomato. Advances in Genetics 8: 267-382.

Robertson, A. 1955. Prediction equations in quantitative genetics. Biometric 11: 95-98.

_____. 1959. Experimental design in the evaluation of genetic parameters. Biometrics 15: 219-226.

Robertson, F. W. 1957a. Studies in quantitative inheritance. X Genetic variation of ovary size in Drosophila. J. Genet. 55: 410-427.

_____. 1957b. Studies in quantitative inheritance. XI. Genetic and environmental correlation between body size and egg production in D. melanogaster. J. Genet. 55: 428-443.

Snyder, R. J. and Larson, R. E. 1955. Quantitative inheritance of seed size in a cross between Lycopersicon esculentum and L. pimpinellifolium. Penn. State Coll. Agr. Exp. Sta. Bull. 607: 24 pp.

Wellington, R. 1922. Comparison of first generation tomato crosses and their parents. Univ. of Minn. Agr. Exp. Sta. Tech. Bull. No. 6: 27 pp.

Yeager, A. F. 1937. Studies on the inheritance and development of fruit size and shape in the tomato. J. Agric. Res. 55: 141-152.