GENETIC STUDIES OF EARLINESS AND GROWTH STAGES OF *LYCOPERSICON ESCULENTUM* MILL.

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ABSTRACT

It is desirable to develop tomato (Lycopersicon esculentum Mill.) cultivars which have the characteristics of earliness to fit the relatively short and cool growing season in Canada. Earliness was studied by partitioning the life cycle of the tomato plant into 7 component growth stages and using these as a basis for attempts to recombine quantitative genes which control the earliness of different stages from different parents to obtain progeny earlier than both parents.

The mode of inheritance of the earliness in the 7 growth component stages was studied with 3 approaches. First, a complete diallel cross experiments used 3 parental cultivars: Bonny Best, Immur Prior Beta and Cold Set. The progenies were grown under 2 temperature regimes (17.0-21.0^{o}C and 10.0-13.0^{o}C). The data for days required for each stage were analyzed first by the Hayman and Jinks method which estimated the following 4 genetic parameters: variation due to differences in additive and dominant gene action; asymmetry of positive and negative effects of genes; relative frequencies of dominant and recessive alleles; and 5 genetic estimators: average degree of dominance; proportion of dominant and recessive alleles; ratio of the total numbers of dominant to recessive genes in the parents; number of effective factors which exhibit some degree of dominance and the heritability.

The calculated genetic parameters and estimators differed in the 2 temperature regimes indicating there could be differences in gene action such as overdominant instead of partial dominant gene action depending on

the temperature conditions. There were differences in heritabilities for the component stages, and some of the longer stages had potentially useful high heritabilities.

The data were also analyzed by the Griffing method which estimated the general combining ability and specific combining ability. The analyses showed that both the additive and dominant gene action had significant effects in most of the component stages, and in most cases, the additive variance was larger than the dominant variance.

The second approach employed reciprocal cross experiments with 2 parental cultivars, Bonny Best and Immur Prior Beta, and their reciprocal hybrids under the 2 temperature regimes in greenhouses and growth chambers. The nuclear and/or cytoplasmic effect on the 7 growth component stages, net photosynthesis rate and leaf area were studied. There was some evidence that cytoplasmic effects were relatively important for some of these characteristics, and these effects were more noticeable in the cool regime.

In the third approach, field selection experiments on the earliness of 2 major stages were commenced in the F_3 of Bonny Best and Immur Prior Beta reciprocal cross populations. The mean values for both stages in the F_5 reciprocal populations were earlier than the 2 original parents indicating recombination of genes for earliness from parental cultivars. These results indicate that the methods which were used in these studies are a feasible way to increase the quantitative characteristic of earliness in the tomato.

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INTRODUCTION

The tomato (Lycopersicon esculentum Mill.) is one of the most important vegetable crops in North America. This crop is strongly thermoperiodic in its environmental response (Went, 1957) and is not well adapted for short and frequently cool growing seasons in Canada, therefore faster growing and earlier crops tolerant to cool temperatures are a primary requisite in the production of Canadian tomatoes. Breeding for increased earliness and cool temperature tolerance has been done for many years, but further improvement for both characteristics is needed in order to have an expanding tomato production program in Canada.

Powers et al. (1950) studied tomato earliness by partitioning the life cycle into 3 stages: a) first stage: seeding to first bloom; b) second stage: first bloom to first fruit set and c) third stage: first fruit set to first ripe fruit. They proposed that recombination of early stages could result in earlier cultivars. These designated first and third stages were relatively long and the genetic mechanisms which controlled these stages still need to be clarified.

For this study, the life cycle of 3 cultivars: Bonny Best, Immur Prior Beta and Cold Set was further partitioned into 7 stages: 1) seeding to germination; 2) germination to first true leaf; 3) first true leaf to flower bud formation; 4) flower bud formation to first flower; 5) first flower to first fruit set; 6) first fruit set to color change; 7) color change to ripening.

The objectives of the present experiments were 1) to evaluate

the 7 growth component stages using the diallel cross technique to estimate gene action, heritability and numbers of genes associated with each stage; 2) to use reciprocal crosses to ascertain whether any differences could be attributed to cytoplasmic effects; 3) to contrast warm and cool temperature regimes inthe genetics studies in the diallel and reciprocal cross experiments and 4) to utilize the genetic knowledge in a field selection program for earliness recombinations in the third to fifth generations.

LITERATURE REVIEW

A. Diallel Crosses

Jinks and Hayman (1953) and Hayman (1954), based on methods of Mather (1949), and using diallel crossing, showed how variances and covariances among pure lines could be used to provide estimates of the overall degree of dominance in the parents, an estimate of heritability and other genetic parameters. Accordingly, the diallel cross technique has been widely used by plant breeders as a method for studying continuous variation. Johnson (1963) pointed out that the diallel cross has 2 main advantages: a) experimentally, it is a systematic approach, and b) analytically, it has a genetic evaluation that is practical for identifying the crosses with the best selection potential in early generations.

Griffing (1956a) showed how the diallel analysis provides information about the variance of general combining ability (σ^2_g) and specific combining ability (σ^2_s). Griffing (1956b) demonstrated that when a set of inbred lines is used in a diallel crossing system, a genetic interpretation in terms of quantitative inheritance is made possible by the fact that the analysis is really a 'gamete' combining ability analysis. Thus in the diallel statistical analysis, the method may regard the genotypic effect of any individual as the summation of effects contributed by each gamete (i.e. set of genes in the gamete) and the interaction of gametes (i.e. the interaction of the genes in one gamete with those in the other).

Kempthorne (1956) criticized the Jinks-Hayman analysis on

the basis that

> "the diallel cross must be interpreted in terms of some population which has given rise to the homozygous parents in inbreeding. If such a population does not exist then the whole analysis is likely to lead nowhere, and also one may question the value of estimating genetic variance, unless the estimated quantities are measures of the characteristic of a definite population".

Since the parents of self-pollinated crops will usually not have been derived by inbreeding from the definite population, Kempthorne evidently considers that the Jinks-Hayman type of analysis of diallel crosses has little practical value as an aid in the improvement of self-pollinated crops. Hayman (1957, 1958 and 1960) has considered these criticisms and has discussed some additional aspects of the theory by removing the restriction that the inbred lines must be fixed. Gilbert (1958) has evaluated the diallel cross, and pointed out that this technique does give more information than that obtained from the parents only: the diallel analysis provides additional information on dominance and recessive relations, on genic interaction, and on probable linkage associations.

The use of the diallel analysis to study quantitatively inherited characteristics of crops has received considerable attention during the last 20 years. Many investigators have applied the Jinks-Hayman and/or Griffing approaches on various crops, including snap beans (Dickson, 1967); cotton (Verhalen et al., 1971; Al-Rarvi and Kohel, 1970); tobacco (Jinks, 1954; Povilaitis, 1966; Legg et al., 1970; Matzinger et al., 1971); ryegrass (Lewis, 1970); forage crops (England, 1968; Fejer, 1971); weeds (Williams, 1962); maize (Eberhart et al., 1964; Poneleit and Bauman, 1970; Rosenbrood and Ankrew, 1971); cabbage (Chiang, 1969); wheat (Allard, 1962; Kronstad and Foote, 1964;

Hsu and Sosulski, 1969; Bhatt, 1971); barley (Johnson and Aksel, 1959); flax (Shehata and Comstock, 1971); linseed (Anand and Murty, 1969).

In tomato, the diallel cross analysis has been applied to many characteristics, such as locule number (Ahuja, 1968; Andrasfalvy, 1971); fruit size (Horner and Lana, 1956; Kheiralla and Whittington, 1962; Peat, 1963; Khalf-Allah, 1970; Andrasfalvy, 1971); yield (Horner and Lana, 1956) and soluble solids in fruit (Stoner and Thompson, 1966).

B. Reciprocal Crosses

In his book "Extrachromosomal Inheritance", Jinks (1964) defined reciprocal crosses as crosses in which the sources of male and female gametes are reversed. When parental lines differ only by chromosomal genes, it is generally unimportant whether these genes go into male or female gametes; the progeny of reciprocal crosses between such parental lines are genetically identical. However, differences in certain quantitative characters between reciprocal crosses do arise. Some examples of such characters are: oil and fatty acid contents, grain yield, maturity, plant and ear heights, and number of ears per plant in maize (Bhat and Dhawan,1971; Garwood et al.,1970); flowering time and plant height in Nicotiana rustica (Jinks et al.,1972); seed protein content in soybeans (Singh and Hadley,1972); in tomato, seed germination (El Hassan,1972); fruit size (Halsted 1918, Cram 1952; Shumaker et al.,1970); early maturity (Li and Hornby,1972; Shumaker et al.1970); early yield (Driver,1937; Meyer and Peacock,1941; Moore and Currence,1950; Cram,1952; Shumaker et al.,1970).

The earliest work on reciprocal breeding in tomatoes was reported by Halsted (1918) on fruit size. He concluded that if a

small fruit cultivar was used as a female parent, the F_1 produced smaller fruit, whereas if the female parent was the large-fruit cultivar, the F_1 produced larger fruit. Moore and Currence (1950) studied 21 pairs of reciprocal hybrids in tomatoes. They found that 6 pairs showed significant differences between reciprocals in early yield, whereas fruit size and total yield differed significantly in thirteen and three pairs respectively. Driver (1937) and Meyer and Peacock (1941) demonstrated differences between pairs of reciprocals for earliness and total yield in F_1 hybrid tomatoes. Cram (1952) claimed that the differences between tomato reciprocal hybrids resulted from some maternal or cytoplasmic influence. El Hassan (1972) reported that the reciprocal differences were found between F_1 and F_2 generations, in tomato, for sprouting at 10.0°C but not at 35.0°C. He concluded that the reciprocal differences were attributable to the contribution of the embryo genotype, maternal effects and interaction of maternal genotype and cytoplasmic effects. Li and Hornby (1972) partitioned the tomato life cycle into 3 growth component stages under 2 different temperature regimes, they found that the days required to complete each of the growth component stages in reciprocal hybrids responded differently.

Evidence for cytoplasmic inheritance has been reported for different plants by many workers including Ashri (1964), Beale (1966), Granick (1965), Katsuo and Mizushima (1958), Koopmans (1959), Michaelis (1954) and Sager (1965).

Bhat and Dhawan (1970, 1971), Brown (1961), Fleming et al. (1960) and Singh (1965, 1966), working with maize, have shown that the expression of some polygenically inherited traits may be governed by the cytoplasm.

Jinks et al. (1972) reported that there are 2 kinds of differences between reciprocal crosses, transient and persistent. These may be maternal or paternal effects. Differences in the maternal environment can give rise to transient reciprocal differences. Such differences are known in the animal kingdom where they were traced to differences in the maternal genotypes (Mather and Jinks, 1971). Persistent reciprocal differences usually arise through unequal contributions of cytoplasmic determinants from the female and male gametes to the zygotes. Such differences are prevalent in the plant kingdom.

C. Selection In Plant Breeding

The history of crops has been influenced considerably by man's augmentation of selection. It was understood that many crop characteristics were being modified by selection.

Walker in his 1969 review, stated that there were only three basic factors of selection even when the genetic situation is highly complex. First, selection operates because some individuals are favoured in reproduction at the expense of others; secondly, selection acts through heritable differences; and thirdly, selection works upon variation already present in the organism. Mather (1953) summarized the effects of selection on a population as being directional stabilizing or disruptive.

Many characteristics such as yield and earliness are easy to measure, but they are the products of interactions at both the genetic and environmental levels. These characteristics have been considered to be basically controlled by genes with small effects, which may be modified by environmental fluctuation and subsequently

the data lead to variable estimates of heritability. Hazel and Lush (1942) showed that selection for a total score is much more efficient than selection for one trait at a time. They also showed that selection for several traits by using indepenent culling levels for each is more efficient than random selection for each trait one at a time. In contrast, Mather (1960) proposed that the selection procedure begin with the partitioning of complex characteristics into subunits (component analysis) and, with the use of biometrical genetics, modify the selection procedure as required. The best results from component analysis have been achieved when subunits act in multiplicative fashion; for instance, the yield of the tomato plant can be expressed in terms of fruit number and fruit size (Gilbert, 1961). Similarly, Powers et al. (1950) partitioned the tomato life cycle into 3 major component stages: 1) seeding to first flower, 2) first flower to first fruit set, and 3) first fruit set to first fruit ripening. They found little evidence that these subunits were determined by a sufficiently small number of loci to permit simple Mendelian analysis. In reviewing their data, it appeared that the biometrical test sometimes showed that the subunits could be considered under more simple control than the complex characteristics of total yield and earliness.

Peirce and Currence (1959) reported on the results of selection for 3 quantitative characters: earliness, yield and fruit size in segregating populations of tomato plants. Their data showed that one generation of selection resulted in a considerable gain in fruit size, a significant increase in yield and little change in earliness. As expected the estimates of heritability for earliness were low whereas the other two characteristics had higher heritability values.

One major selection system developed to maintain a higher level of genetic variability within the breeding population is recurrent selection. This system has been proposed as a promising method for effecting stepwise changes in gene frequency within a population as opposed to the development of inbred lines which gave homozygosity under continuous self-pollination. Comparative studies conducted by Comstock et al. (1949), Lonquist and McGill (1956), Sprague et al. (1952) have demonstrated the superiority of recurrent selection over selection within self-fertilized progenies. The rapid approach toward homozygosity apparently did not allow adequate opportunity for selection; therefore, Allard (1960) suggested that some less intense form of inbreeding, such as sib-mating might aid in the selection of superior genotypes from a given foundation population. Khalf-Allah and Peirce (1964) applied this method in tomato and found that the progenies developed by sib-mating generally maintained higher genetic variability for fruit size, earliness and total yield than did self pollinated selections. Recurrent selection has also been applied to improve the specific combining ability of breeding lines in many other crops, especially in maize (Hull, 1945; Horner et al., 1972).

The difficulty arising from selection for a single trait is the genetic and environmental correlation with other traits, but this can be partially resolved by the use of a selection index. Such an index has been widely used by the animal breeders, but has been little used by the plant breeders. Andrus and Bohn (1967) used an index in a mass selection program with muskmelon. This index was a simple scoring method with equivalent economic weight attached to each character. Plants with the largest total score or highest index were selected. Peirce (1968) reviewed selection procedures and the problems

involved. He noted that the estimates of parameters used to construct an index are usually different for each cultivar population in a breeding program, and these estimates, particularly of genetic correlations, are subject to considerable error. He states that

> "The concept of selection by index is a viable one and should not be discarded".

He also stated that

> "An index is particularly suited to those crops in which value is determined by readily measureable attributes. And for those measureable characters contributing to the balanced genotype, affected by difficult correlations, an index may help".

Another aspect that must be considered by the plant breeders as affecting selection is the magnitude of the genotype/environment interaction. Allard (1964) summarized this problem as follows:

> "The genotype and environment interaction is always a component of variation. Interactions, such as variety x location, variety x treatment are frequently predictable, and one can usually breed plants that will excel in a specific environment. The variety x year effects are not predictable, and the breeders must attempt to minimize the impact of such interaction by testing varieties over a series of years and locations".

Further emphasis on this interaction was expressed by Comstock and Moll (1963) as follows:

> "Because genetic facts are inferred from observations on phenotype, because selection is based on phenotype and becaused there is a potential contribution of genotype and environment interaction effects on the phenotype of all quantitative characters; genotype x environment is in some way involved in most problems of quantitative genetics and many problems of plant breeding, therefore, all of its possible implications deserve attention."

D. Growth Component Stages And Temperature Effects

1. Stage 1: From Seeding to Germination

In earlier studies, variation in the rate of seed germination

at different temperatures has been observed in many vegetable crops. Kotowski (1926) reported that speed of germination for 17 different kinds of vegetables increased as the temperature rose. The optimum temperature for tomato was 18.0°C and the minimum was between 11.0°C and 18.0°C. Went (1957) found the time required for tomato seed germination depended greatly on temperature, and the lower the temperature then the longer the time required for germination. Whittington et al. (1965) reported that time for germination showed a genetic component, but the relationships between different genotypes was much influenced by environmental factors. The effect of temperature on seed germination was highly significant, and the time required for germination being greatest at the lower temperatures. Whittington and Fierlinger (1972) indicated the inheritance of time to germination of tomato seed was largely additive and closely related to seed size. Pollack and Larson (1956) indicated that speed of tomato seed germination depended primarily upon environmental factors, and that within one cultivar seed size has little or no effect.

The existence of genetic differences in the capability of tomato seed to germinate at low temperature has been mentioned by various investigators. Smith and Millett (1964) reported that significant differences were observed among 10 varieties at constant temperatures of 15.0°C and 10.0°C but not at 20.0°C. Kemp (1968) reported that the ability of some tomato cultivars, such as 'Earlinorth' and 'Rocket', to germinate at low temperatures may be inherited; and at 10.0°C or lower, the percentage of germination of all cultivars was reduced significantly. Berry (1969) reported differences in germination response at 35.0°C and the existence of a heritable association

between high and low temperature response. El Hassan (1972) reported that sprouting at 10.0°C, germination percentage at 35.0°C, and rate of germination at 35.0°C are inherited characters and controlled by at least 3, 2 and 1 gene(s) respectively. He also reported a high correlation between germination at low and high temperatures and the probable existence of 2 different genetic systems which are recombinable. Cannon et al. (1973) reported the ability of tomato line PI 341988 to germinate at 10.0°C is controlled by a recessive gene (ltg). El Sayed and John (1973) pointed out that germination of tomato seed needs at least the accumulation of 160 daily heat units. They found the characteristic of germination at low temperature for the F_1 and F_2 progenies was intermediate between their contrasting parents. Inheritance was found to be quantitative and an estimate of 24 gene pairs differentiated the parents for germination. There was strong evidence for additive gene action although dominance and epistasis were not ruled out. They also indicated that the same gene system appears to control emergence of seeds at both low (10.0°C) and high (20.0°C) temperatures with a heritability of 25-40% and selection for emergence at low temperature could be achieved at high temperature. Phatak (1970) indicated that the seed from plants selected for normal germination at 10.0°C night and 12.0°C day showed a definite improvement in cold germinating ability.

2. Stage 2: From Germination to First True Leaf Appearance

Variation in growth of the seedling could be expected to be influenced by initial embryo size (Ashby 1930, 1937). However, East (1936), Luckwill (1939) and Hatcher (1940) found that some tomatoes which showed heterosis for early seedling growth did not have any

apparent difference in embryo size and concluded that the size of the embryo was not the index of heterosis. Whaley (1939) made a study of growth rates of the parents and hybrids in two Lycopersicon species crosses showing heterosis. In both crosses the hybrids grew faster than either parent in the early post-embryonic stage, he also noted that heterosis was not always accompanied by the possession of a larger embryo in the hybrid. In a second paper (1939) he presented evidence showing that there was no relationship either in the embryo or during development, between the volume of the apical meristem and heterosis. Whittington et al. (1965) using hybrids from L. esculentum and L. pimpinellifolium found that the hybrid hypocotyl although its emergence was delayed by later germination, came to exceed in length that of L. pimpinellifolium. Since hypocotyl extension in tomatoes in the dark is by cell elongation rather than by cell division, it is likely that this result is due to an enhanced rate of extension of individual cells in the hybrids. It was thought that the significant difference between the parent and hybrid was due to the greater cell number in the hybrid hypocotyl.

3. Stage 3: From First True Leaf to Flower Bud Appearance

(A) Leaf Development

Throughout the history of research on crop plants many workers have sought to find some observation or system of measurements that would accurately reflect the growth response caused by the environmental factors, for instance, fluctuation of temperature has been evaluated in various ways with respect to the effects on plant growth such as plant height, leaf area, phenological development, etc. As early as 1735, Reaumur attempted to correlate changes in temperature

with plant development. Since then, the resultant correlations of growth and temperature data were developed. Went (1944, 1945), Verkerk (1955), Lewis (1953), Calvert (1958, 1959) have demonstrated that the early development of the tomato is affected by the temperature and light intensity during the first few weeks from germination. Calvert (1957, 1959) has shown that the number of leaves formed between the cotyledons and the first inflorescence, increases with temperature but decreases with light intensity. Hussey (1963) reported that temperature had a greater effect on leaf growth than on leaf number; however, more leaves were formed before flowering at 25.0°C than at 15.0°C. He also observed the effects of high temperature in delaying the enlargement of the apex and of increasing the number of leaves produced before flowering.

The day and night temperature requirements for the tomato were investigated by Went (1944) who found that optimal growth occurs when the temperature during the dark period is lower than that during the daily light period. This kind of temperature response, he termed thermoperiodicity. Hussey (1965) indicated that the average day temperature affected leaf growth one and half times as much as night temperature.

To establish the process which controls the growth of tomato plants is of some interest, because it may assist the plant breeder in choosing the direction for developing improved cultivars. Went (1944) studied the correlation between various physiological processes and growth in the tomato plant. He found the elongation rate of tomato stems decreased sharply during the day, and photosynthesis reached its optimum near 10,764 lux and was only slightly lower at 18.0°C

than at 26.5°C, but was significantly lower at 8.0°C. Translocation of sugars was low at 26.5°C, and steadily increased as the temperature decreased to 8.0°C.

(B) Plastochron

In developmental studies one can usually relate only the simplest aspects of the developing organism or organ to time directly. The term 'plastochron' proposed by Askenasy (1880) has gained fairly wide usage (Esau, 1953). She defined plastochron as:

> "The period between initiation of successive leaves in the shoot of a higher plant which appear periodically".

When successive plastochrons are equal in duration, the plastochron may be made to serve as the unit of a developmental scale. Erickson and Michelini (1957) defined a plastochron as the time interval between initiation of two successive leaves. Thus the plastochron might be more broadly defined as the interval between corresponding stages of development of successive leaves, and one might choose initiation, maturity or any intermediate stage of development as the stage of reference.

(C) Photosynthesis

The yield of each agricultural crop is directly affected by the rate and production of photosynthesis. The production and the rate of photosynthesis are affected by the soil and climatic conditions, especially the latter; for example, light (Porter, 1937; Talling, 1961; Hesketh and Moss, 1963; Hesketh and Baker, 1967; Peat, 1970; Scott et al., 1970); temperature (Wassink, 1945; Kramer and Kozlowski, 1960; Alberda, 1969; Hew et al., 1969; Machold, 1969; Treharne and Eagles, 1970); CO_2 concentration (Gaastra, 1962; Brun and Cooper,

1967; Bishop and Whittingham, 1968).

In spite of the importance of photosynthesis, no serious attempt was made until recently to establish the genetic variability in photosynthetic efficiency among crop plants. A plant breeder must understand thoroughly the masking effect of the various factors (both external and internal) regulating photosynthetic rates and in turn obscuring the genetic potentiality of this character in crop improvement programs. The evidence for genetic variability of photosynthetic efficiency among species has been demonstrated in numerous studies. Hesketh (1963) and Hiesey and Milner (1965) reported differences in photosynthesis amongg species such as Ricinus communis L., Helianthus annus L., Zea mays L., Dactylis glomerata L., Trifolium pratense L., Acer saccharum Marsh., and Quercus rubra L. Differences for photosynthetic rate have been shown among cultivars within a species as inthe case of rice (Noguti, 1941); barley (Ekdahl, 1944); wheat (Asana and Mani, 1950); cotton (Muramoto et al., 1965); blueberry (Forsyth and Hall, 1965); sugarcane (Irvine, 1967); oats (Jennings and Shibles, 1968; Lawes and Treharne, 1971);sorghum (Eastin and Sullivan, 1969); alfalfa (Pearce et al.,1969); bean (Wallace and Munger, 1966); maize (Duncan and Hesketh, 1968; Garg et al., 1969); tobacco (Zelitch and Day, 1973).

In tomato, Stambera and Petrikova (1970) found a difference in photosynthetic rate between determinate and indeterminate tomato varieties, and they also found that the high efficiency of the assimilative apparatus can be observed in the period from the beginning of flowering till the beginning of fruit formation. Breznev and Tagmazjav (1969) reported that in the majority of hybrids, photosynthetic activity during bud formation and flowering was higher than in the

parental varieties and that the hybrids were superior in yield. Kirk and Tilney-Bassett (1967) indicated that there was the possibility of genetic control of formation of photosynthetic apparatus in the plastid, which apparently influenced the photosynthetic rate among the cultivars. They also discussed a number of instances of mutations in nuclear genes which might possibly be regulator genes, as for example, the green-flesh and the lutescent mutations in tomato.

Went (1957) pointed out that under normal field conditions young tomatoes probably lose less than 10 percent of their photosynthates in respiration, the remaining 90% going into the building of the tomato plant and fruit growth. Evans (1969) was of the opinion that photosynthetic rate constituted the primary limitation to productivity in tomato under most conditions. Donald (1962) expressed the opinion that plant breeders have been paying insufficient attention to photosynthesis as a basic process affecting crop yield. Also he pointed out that plant form or habit can affect photosynthetic gain. Moss (1969) indicated that breeding for photosynthetic efficiency requires the identification of desirable parental stocks. Non-genetic variability on photosynthetic measurements is important. When measuring the photosynthetic rate, one has to consider the environmental effects and try to control this variation. Kristoffersen (1963) pointed out that the net photosynthesis in tomato was so greatly affected by environmental fluctuation during the time periods used to make the measurements, that the net photosynthesis rate from such procedures were inefficient for identifying parental lines with the genotypes for high net photosynthesis rates.

(D) Flower Initiation

There are several reports about the influence of temperature and light on floral initiation in the tomato. Went (1944) reported that the optima of normal day temperature and lower night temperature did not materially increase or decrease the number of flowers initiated per inflorescence. Phatak (1966) compared two regimes, 15.5°C to 18.5°C and 18.5°C to 21.1°C during the period from the seedling to the appearance of the first inflorescence, and reported that the number of flowers was significantly increased under the cooler regimes. Lewis (1959) reported that temperature was the main factor which affected the number of flowers in a tomato inflorescence. He also indicated that alternation of warm days and cool nights, and vice versa, as opposed to a uniform temperature, had no effect on flower number in plants grown under natural light, but both temperature combinations had a depressing effect on flower production under artificial light. Wittwer and Teubner (1956) and Calvert (1958) reported that earliest flowering was initiated when the day and night temperatures were equal. Lake (1965) suggested that various plant processes such as vegetative growth, flower initiation, floral growth and fruit growth may have different temperature requirements.

4. Stage 4: From Flower Bud Appearance to First Flowering

Wittwer and Aung (1969) reviewed the development of the tomato flower and indicated that a small protuberance of meristematic tissue develops from the pedicel of the preceding flower. The portion of this pedicel posterior to the protuberance becomes part of the peduncle. The meristematic protuberance or axil for the first flower of the cluster originates in the axil of the leaf. The pedicel which

supports a single flower, as well as the peduncle from which it arises, is composed of a rather thick cortex, a ring of vascular tissue and a central portion of pith tissue (Cooper, 1927). Smith (1935) similarly observed that the protuberance of the first flower of the inflorescence arose in the axil of the leaf. The succeeding flowers of the cluster each arise from similar protuberances which grow out from the pedicels of the preceding flower.

There are reports about the environmental effects of temperature on flower development. Zielinski (1948) reported that low temperature environment (7?28°Cand 12.8°C) influenced perianth development in the tomato, resulting in fasciation of perianth components, and frequently in adhesion of stamens to the corolla or calyx and and cohesion of the antheridial filaments. Rudimentary anther sacs with aborted pollen occurred frequently. Rick (1946) observed that under cool temperature, tomato flowers often drop without setting fruit, and one of the main reasons may be abortion of the pistil.

5. Stage 5: From First Flower to Fruit Set

Although the days required for this stage are relatively few, there are several developmental processes which occur during this stage. Besides the existence of viable pollen in the anthers, there is the need for transfer of pollen from the anthers to the stigma, pollen germination, pollen tube growth, fertilization and early fruit development.

A comprehensive study of factors affecting sporogenesis and the development of pollen grains was made by Howlett (1936). Using cytological techniques he found that under conditions of severe carbohydrate deficiency, sporogenous tissue in some anthers failed to

reach meiotic division. In addition to this early effect, degeneration of mature pollen grains was also a frequent occurrence (Calvert, 1964). Anthers which were subnormal in size and were not the normal deep yellow color invariably contained only sterile pollen grains. Went (1957) indicated that abnormal pollen was produced when temperatures were lower than 13°C, and he considered this to be the major factor causing unfruitfulness in tomatoes grown at low night temperatures. On the other hand, pollen can be produced normally, but may not be released from the anthers due to morphological abnormalities. Larson and Paur (1948) studied this functional male-sterile tomato, and reported that the connate form of the petals resulted in considerable constriction of the anthers and tended to hold them in close contact with the pistil, thus preventing rupture of the stromium and the subsequent release of the pollen.

The position of the stigma within the anther tube and the internal dehiscence of the anthers favors a high degree of self-pollination. A number of workers have observed that with certain cultivars in certain environments, the stigma may project beyond the opening of the anther tube, (White, 1918; Bouquet, 1919; Smith, 1935). More recently Williams (1960) observed that both day length and temperature affected the ratio of carpel length to stamen length. He also observed the degree of unfruitfulness likely to result from stigma exsertion, for example, one cultivar which had a carpel length/stamen length ratio of 1.12 set only 16.2% of flowers, whereas another cultivar with a ration of 0.96 set 60% of the flowers.

The time of dehiscence and the period during which the stigma remains receptive are critical factors in the pollination and

fertilization of inbreeding species such as the tomato. Smith (1935) stated that in summer the corolla remained open and the stigma receptive for about 4 days. Judkins (1940) found the stigma to be receptive about 2 days before anthesis, and a period of 2-3 days usually elapsed between pollination and fertilization at normal greenhouse temperatures (16.0-20.0°C). Koot and Ravestijn (1963) found the receptivity of the stigma to be adversely affected by dry sunny weather, but in dull humid weather little pollen was liberated from the anthers.

The receptivity of the stigma and the ability of pollen to germinate appears to be strongly influenced by temperature. Experiments in which pollen was germinated at 4 temperatures, namely 10.0°, 21.1°, 29.4° and 32.8°C were reported by Smith (1935) and Smith and Cochran (1935). They found that pollen remained inactive for several hours after being deposited on the stigma. At 21.1° and 29.4°C short tubes formed after 6 hours, but at 32.8°C only 0.1% of the pollen had germinated during the first 12 hours and only 3.9% after 84 hours. Germination was best at 29.4°C but only slightly better than 21.1°C. Koot and Ravestijn (1963) assessed the degree of fertilization by the percentage of pollen grains germinating on the stigma 2 hours after pollination. They found that both the degree and speed of germination were largely dependent on temperature. Dempsey (1969) reported tomato pollen germination occurred after 40 minutes at 35.0°C, and at 5.0°C the time was increased to 20 hours. Hornby and Charles (1962) reported that the need for a minimum size of pollen application, and noted cultivar differences in the minima.

After germination of the pollen grain, growth of the pollen tube through the style is the most important part of the sequence

of events during the progamic phase of fertilization. Tube growth is concerned with protein synthesis, formation of wall material, as well as oriented growth toward the micropyle of the embryo sac. For external factors, temperature was found to have a marked effect on the germination percentage of pollen as well as on the rate of pollen tube growth. The maximum rate of pollen tube growth occurred at 21.1°C with 29.4°, 10.0° and 32.0° ranging in decreasing order (Smith and Cochran, 1935). Preil and Reimann-Philipp (1969) reported that the pollen tubes reached the ovary in about 12 hours at 20.0-25.0°C and in 48 hours at 10.0°C. Temporary low temperature (0°-2.0°C/15 hours) did not injure the pollen tubes and they began to grow again when the temperature had risen. Judkins (1940) reported the time involved in pollen tube growth appears to increase during the fall and winter when light is of low intensity. Dempsey (1969) stated that the extensive pollen tube growth only occurred in the 10.0-35.0°C range. At 37.0°C pollen tubes grew abnormally and later ceased growth while in the style. He concluded that growth was inversely related to temperature because pollen tubes entered the micropyles 7 hours after pollination at 35.0°C but required 34 hours at 10.0°C.

The sequence of events between pollination and fertilization was carefully observed and reported by Smith (1935). About 50 hours after pollen reached the stigma, one of the male nuclei fused with the polar nuclei, the other fusing with the egg. After fertilization the zygote did not begin division for 36 to 48 hours. The embryo sac greatly enlarged in the meantime. The primary endosperm nucleus began division in advance of the embryo. At 66 hours after pollination, when the zygote was still a single cell, the endosperm

consisted of 8 cells with definite walls separating them.

6. Stage 6: From First Fruit Set to First Change of Fruit Color

There has been considerable discussion and speculation on the general problem of the fruit setting and the development of young fruit in relation to the growth of the plant and different factors of the environment. Shan'gina (1961) stated that relatively poor fruit set on the lower truss of the tomato may be attributed to the small storage reserves in plants grown under the poor light conditions of early spring. Such nutritional deficiencies have been suggested as the possible cause of failure or poor set for the first inflorescenses to produce fruit in tomato after transplanting (White, 1930; Rick, 1946; Leopold and Scott, 1952). Murneek (1939) pointed out that food reserves are of great importance in the initiation and development of the reproductive phase in tomato plants.

Regarding the environmental effects, Went (1944) reported that in the first and second clusters, fruit set was abundant only when the night temperatures were between 10.0° and 20.0°C; and with lower or higher night temperatures, fruiting was reduced or even absent. Lake (1965) studied the temperature effect on fruit setting, and claimed the day temperature appeared more important than the night temperature. Robinson et al. (1965) reported that cold temperature appeared to affect fruit setting of tomato primarily through its influence on microsporogenesis. They also reported that high temperature had a similar effect, suggesting that the same genetic system determined fruit setting response to either high or low temperatures. This cool temperature effect on fruit set was also reported by Learner and Wittwer (1953), Calvert (1958), Wedding and Vines (1959), Schaible

(1962), Curme (1962) and Lake (1967).

Most varieties of tomatoes will produce parthenocarpic fruit at a relatively low temperature, but not at relatively warm temperature. Osborne and Went (1953) found parthenocarpic fruit at a low temperature with a high light intensity. Daubeny (1955) found that poor pollen germination and/or growth may explain the parthenocarpic fruit produced by tomato cultivar Bonny Best at the cool temperature (10.0° to 12.8°C) despite hand pollination.

Leopold and Scott (1952) pointed out that tomato fruit set was strongly and quantitatively dependent upon the presence of mature leaves. Darkened mature leaves were less effective than lighter ones for promoting fruit set.

Agreement has not been reached as to the stage of development at which mitosis actually ceases in the developing fruit. Smith and Cochran (1935) reported that cell division proceeded actively in the fruit flesh for approximately 2 weeks after pollination. Houghtaling (1935) as well as Gustafson and Houghtaling (1935) concluded that fruit growth after pollination was a result of cell enlargement only. MacArthur and Butler (1938) reported that ovary growth was entirely by cell division prior to pollination, and that subsequent growth was chiefly by cell expansion, cell division being a minor factor that just sufficed to maintain the tissue containing non-expanding epidermal cells. Groth (1910) had previously reported that young and mature fruits contained the same number of epidermal cells, and that mitosis played little part in the enlargement of the tomato fruit skin. Clendenning (1948) reported that growth of the fruit includes a phase of residual mitotic activity that persists for

approximately 1 week after setting.

There is a relationship between fruit position within the truss and fruit growth. Beadle (1937) considering the first 6 fruits in the trusses of cultivar Kondine Red, found that the nearer the fruit was to the main stem then the shorter was the maturation period. Similar reports were made by Kidson and Stanton (1935), Kerr (1955) and Cooper (1959).

There are also some relationships between growth rate, size of fruit and other physiological characters. Cooper (1959) pointed out that fruits which begin to swell rapidly at the beginning of fruit development have a shorter maturation period than those fruits which have a period of initial lag before rapid growth begins. Gustafson and Stoldt (1936) pointed out that increasing the leaf area, can result in the size of fruit being increased after the time of setting. Clendenning (1942) reported that the growth of fruit was found to be associated with an absolute increase in respiration rate.

7. Stage 7: From First Change in Fruit Color to Fruit Ripening

Color changes in tomato fruit are the most obvious signs of ripening. These changes are primarily due to degradation of the chlorophylls and the synthesis of carotenoid pigments. Duggar (1913) and Sando (1920) reported that normal temperature and oxygen supply were the essential requirements for fruit ripening. High temperatures over 32.0°C and low temperatures under 10.0°C were reported to delay or even halt the ripening (Tomes, 1962; Pharr and Kattan, 1971; Walkof, 1962).

Additional to the color changes in ripening fruit, Pattersen (1970) emphasized two major changes: 1) textural changes resulting

from environment and cultural practices that affect cell morphology during growth; and 2) flavor changes in which there is a perception of a combination of sweetness, acidity and astringency in conjunction with the odorous volatiles.

E. Genetic Analysis Of Growth And Earliness Of Tomato

Investigations on size and shape in the development of plant organs have given further insight into the more fundamental aspects of their inheritance. Kheiralla and Whittington (1962) and Mallah et al. (1970) pointed out that significant differences in growth rates were found between cultivars and between the reciprocal inter-specific hybrids, and that later this growth rate was found to be inherited additively with a large dominance component (Peat and Whittington, 1963). Kheiralla (1961) reported that delayed germination of L. pimpinellifolium x L. esculentum relative to L. pimpinellifolium may allow a relatively greater translocation of reserves to the shoot of the hybrid. The growth rate of the hypocotyl in this hybrid was found to be higher for a limited period prior to emergence. This may be an explanation for the "undefined biochemical superiority" which Lewis (1953) suggested resulted in the hybrid having a shorter "lag phase" in the attainment of its growth rate.

Luckwill (1939) and Kheirall and Whittington (1962) comparing hybrids and their parents reported that the hybrids had a larger leaf area which was related to a greater fruit yield. Whaley (1939) pointed out that the leaves of hybrids were intermediate in size between parents and tended to be greater than the mean of the parents. Mallah et al. (1970) reported that a dominant gene action was found in the

inheritance of leaf area, whereas for fruit size both dominant and additive gene action were present.

Whaley (1939) reported that the size of flower in tomato hybrids was intermediate between those of the parents. Somewhat similar results were reported by Williams (1959), who found that none of the tomato hybrids exceeded the better parent for such characteristics as number of flowers, fruit size and number of fruits; with the one exception of yield per plant.

The study of earliness led Powers and Kyon (1941) to partition the following 3 stages of the life cycle, 1) seeding to first bloom; 2) first bloom to first fruit set and 3) first fruit set to first ripe fruit. Later Powers et al. (1950) concluded from the use of 2 parental cultivars and their hybrids that the first 2 stages were each controlled by 3, and the third stage by two major gene pairs. Honma et al. (1963) reported that only 1 major gene pair controlled the first growth stage.

Burdick (1954) reported that the time of flowering for hybrids was approximately intermediate between the parents. Similar results were also reported by Williams (1959) and Young (1966).

The opinions about the genetic mechanisms controlling component stages are varied. Corbeil (1965) found that early maturity genes were completely dominant to their late phase alleles in the second and third stages and partially dominant in the first stage. Peat and Whittington (1965) and Mallah et al. (1970) found additive gene action with various degrees of dominant gene action for the first stage. Young (1966) claimed that dominant gene action for the first stage was lacking.

Burdick (1954) stated the following:

> "The maturity genes of both parents appear to be expressing themselves, at different stages in some hybrids. This would support the view that dominance is a relative phenomenon, depending on the stage of development and the environmental circumstances under which it is measured, and that the excellence of hybrids may be attributable to the co-expression of the alleles from both parents, made possible by the existence of dominance along with ontogenetic and environment gradients."

Burdick's idea was supported by Li and Hornby (1972) who showed that certain hybrids exhibited earliness heterosis under a cool temperature environment (10.0°-12.0°C) but responded intermediately between parents under normal culture temperature conditions (19.0°-21.0°C).

A number of workers have reported an association between earliness and certain other tomato characters. Alpat'ev (1957), Daubeny (1959) and Yeager and Meader (1937) reported that selection based on early flowering was the most efficient method isolating early tomato segregates. Bernier and Ferguson (1962) studied the relationships of developmental characters of the tomato with earliness, and they found that the days to first flower (Stage 1) were negatively correlated with earliness (Stages 1, 2 and 3) for the cultivars 'Imun Prior' and 'Early Lethbridge'. Days required for Stage 3 were not correlated with earliness except for the cultivars 'Earlinorth' and 'Early Lethbridge', therefore they concluded that Stage 3 cannot be regarded as a good index of earliness.

MATERIALS AND METHODS

MATERIALS

Three true breeding tomato cultivars which were used as parental lines, and all possible combinations of their crosses were evaluated.

The parental lines were Bonny Best (B), Cold Set (C) and Immur Prior Beta (I). They have the following history and characteristics.

1. Bonny Best (B)

According to Boswell (1933) this cultivar was introduced by the firm of Johnson and Stokes of Philadelphia, U.S.A. in 1908. It is very well known on the North American continent. B has indeterminate growth habit with round, fleshy and uniform colored fruits. Boswell (1933) pointed out that maturation of B fruit was delayed considerably under cool temperatures or other unfavorable conditions. Typically, there are 4 or 5 flowers per cluster with 2 or 3 fruits being set per cluster. This cultivar was used because in the past years a considerable amount of research has been done, in which this popular cultivar was the test plant.

2. Cold Set (C)

It is a relatively new tomato cultivar for direct seeding, developed by Professor T. O. Graham, at the University of Guelph, Ontario, Canada and released in 1962. It came from a cross between Fireball and Filipino #2. Both of C's parents are tolerant to very warm

and cold temperatures. Young (1963) reported that it is resistant to cold temperature, and will set fruit at a night temperature of 7.2°C. This cultivar can set its flowers under both cold and warm conditions. It also has indeterminate growth, and uniformly colord fruit of medium size.

3. Immur Prior Beta (I)

The origin of this cultivar is not known. Curme (1968) and Reynard (1968) believed that this cultivar was developed by Dr. A. Kallio, University of Alaska at Fairbanks, Alaska, U.S.A., however Kallio (1968) said he obtained the seed in 1951 from the Horticulture Department of the University of North Dakota, U.S.A., and he also thought that this cultivar might have come from Europe. This cultivar has the potato leaf trait. It is indeterminate in growth habit, and is very tolerant to low temperatures (e.g. 10.0°C-12.0°C) for fruit set and vine growth. The fruit is relatively small (60-90g) with flattened globe shape, somewhat angular with green shoulders. Dinkel (1966) stated that this cultivar is one of the best for summer production in heated glass houses in the Alaska latitudes.

The three parental lines were crossed in all possible combinations, thus there were six F_1 hybrids. For convenience, these six diallel cross hybrids were abbreviated with the female parent indicated first as follows: BxI, (BI); IxB, (IB); BxC, (BC); CxB, (CB); CxI, (CI); and IxC, (IC).

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METHODS

A. Greenhouse Experiments

1. Experiment I

A diallel cross experiment employing the 3 parental and 6 F_1 hybrids was conducted in the winter of 1969-1970 to observe growth stages under 2 temperature regimes. One greenhouse was kept in the optimum range of 17.0°C-21.0°C and was considered to be the warm regime, in contrast to the second house which was kept in the 10.0°-13.0°C range and considered to be the cool regime.

Seeds were sown on October 20 in each of the 2 greenhouses. Seedlings were pricked out 2 weeks later and set in 5 x 5 cm veneer bands in flats. Temperatures in the 2 houses were recorded on thermographs throughout the experiment (Table 2 in Appendix). On November 30, the plants were placed in the soil beds in 2 greenhouses. The plants were 50 cm apart within the row and 45 cm between the rows. Supplementary light was provided by 4 300-watt fluorescent tubes installed in pairs over the soil beds to ensure a 14-hour photoperiod. Pollination was allowed to occur naturally.

A randomized block design was used with 4 blocks of 1-plant per plot for each of the 9 lines (see Table 1, Appendix).

Earliness was recorded as the number of days required for each of the following:

Stage 1: seeding to germination - germination was recorded when 50% of the total of 50 seeds per line had emerged and expanded their cotyledons to a horizontal level.

Stage 2: germination to first true leaf emergence - which was

considered to be when the first true leaf had reached a length of 10mm.

Stage 3: first true leaf to flower bud emergence.

Stage 4: flower bud emergence to first flowering - the flower was considered open when the corolla was bright yellow and had begun to reflex.

Stage 5: first flowering to first fruit set - which was considered to be when the first fruit had reached a diameter of 5mm.

Stage 6: first fruit set to fruit changing color - when the first orange-pink color was shown at the blossom end.

Stage 7: fruit changing color to fruit ripening - when the color hadd changed to red, the fruit was considered to be ripe.

In Stage 3, the interval between first true leaf to flower bud emergence was subdivided into plastochron units. The first plastochron was considered to be the age when the plant's first leaf had reached the length of 10mm. When the second leaf reached the length of 10mm, it was considered to be plastochron two, and so on. The number of days were also recorded for the intervals between plastochrons.

2. Experiment II

The second experiment was done in the winter of 1970-1971 and the purpose of this experiment was to further the study of Stages 5 and 6 by using controlled pollination procedures to ensure that all the lines had a uniform starting point for their fruit development. The flowers were emasculated 1 day before anthesis by taking away petals and anthers with a pair of tweezers. Pollen was collected

on microscope slides, and transferred to the stigmas with a needle. The date of hand pollination was considered as the first day of Stage 5. The second and third flower of the second cluster were used for this experiment. When the fruit reached 5mm diameter, it was considered as the first day Stage 6. When ripe, the individual fruits were weighed and measured for diameter.

The management regimes including temperature differentials for this experiment were similar to those in the first experiment. Seeds of the 9 lines were sown on Novemberr 1, and the plants were set in the soil beds on December 12. The same design was employed as in Experiment I with a new randomization (see Table 3, Appendix).

3. Experiment III

This experiment used a larger population size but had to be limited to the two more promising parental cultivars, B and I, and their reciprocal hybrids. The management regimes including temperature were similar to those in the first 2 experiments. Seeds of the 4 lines B, I and their reciprocal hybrids were sown on October 29, 1971. Plants were set on the soil beds on December 9 and a randomized block design was arranged with 10 blocks of the 4 lines. There was 1-plant per plot (see Table 5, Appendix). The same data were collected as in Experiment I.

B. Growth Chamber Experiments

1. Experiment I

This experiment was conducted to contrast the response of the plant materials at the cool temperature of 12.0°C with the more optimum one of 21.0°C. Seeds of 3 parental lines and their 6 diallel

hybrids for a total of 9 lines were sown on May 11, 1970. Seedlings were pricked out and set in 7x7 cm plastic pots and placed in growth chambers until the eighth plastochron stage was reached when the experiment was terminated. There was only one replication per line per plastochron. The plants were shifted around within the chambers every other day to minimize the environmental effects.

Data were collected for plastochron ages starting from the 4th to 8th inclusively. Plants were watered at 9:00 a.m. and net photosynthesis rate was measured at 10:30 a.m. An L/B Infrared Analyzer (Beckman model 15A) was used. The leaf area was measured in an airflow planimeter.

2. Experiment II

This experiment used a larger population size than in Experiment I, but was limited to the more promising parental cultivars B and I, and their reciprocal hybrids. Plants of the 4 lines were arranged at random in the growth chamber with 4 replications for each plastochron. Seeds were sown on May 1, 1971 and the management was similar to that in Experiment I, and similar data were collected on the 4th to 8th plastochrons inclusive.

C. Field Experiments

1. Experiment I

This experiment was conducted in 2 parts in field plots at The University of British Columbia in the summer of 1971. The first part comprised B and I and their reciprocal crosses, for a total of 8 lines (B, I, BI, IB, BIxI, IBxI, BIxB, IBxB). Twelve plants per line were used. The seeds were sown on April 13, and

transplanted to the field on May 10. This planting was about 1 to 2 weeks earlier than gardeners would set out plants, and it was expected that the plants would be under test to ascertain whether the plants could set fruit in the less than optimum growing conditions.

The data were recorded for this and subsequent field experiments on individual plants as number of days required for each of the following stages:

Stage A: seeding to first flowering - the flower was considered open when the corolla was bright yellow and had begun to reflex.

Stage B: first flowering to first fruit set - the fruit was considered set when the diameter reached 5mm.

Stage C: first fruit set to fruit ripening - a fruit was considered ripe when the fruit color changed to red.

Since Stage B is very short relative to Stages A and C, it was assumed that Stage B may not be as important as Stages A and C in breeding for earliness, therefore Stage B was not considered for further study.

The second part was used to observe the segregation of F_2 and F_3 from IB and BI reciprocal crosses, and additionally to do selection among the F_3 plants. The selection was for earliness and tolerance of early spring cool temperatures. There were 6 and 11 plants selected in the IB and BI lines respectively. The selection criteria in this 2nd part of the experiment were for segregates which were earlier than both parents, B and I, in Stages A and/or Stage C.

2. Experiment II

The selected plants from the F_3 generation of reciprocal

populations IB and BI were reproduced and evaluated. Thus there was the F_4 for 6 lines from IB selection and 11 lines from the BI selection plus two parents I and B, to give a total of 19 lines in this experiment. Seeds were sown on March 30, 1972 and transplanted to the field on May 15. There were 5 plants per plot, 19 plots per block and total of 5 blocks. The experimental design of the randomized complete block is shown in Table 8 of the Appendix.

3. Experiment III

This field experiment was conducted in two parts. In the first part, seeds from the earliest 10% of the F_4 of the IB and BI lines, which were pedigree selected in Experiment II, were used in a simulated mass selection programme. Equal amounts of seed from the earliest 15 plants selected in the F_4 of the IB line were mixed and a sample of the mixture was used to grow 125 plants which was the F_5 of the IB line. Similarly, seeds from 25 plants of the F_4 of the BI line were mixed, and 250 plants were grown to provide the F_5 of the BI line.

In the second part, selected individual plants for earliness were compared to the individual plants selected for lateness in the F_4 generation. There were 6 plants from the F_4 generation selected for earliness and 2 plants selected for lateness. These represented the extremes in the F_4 population. Seeds were sown on March 30, 1973 and transplanted to the field on May 11. Plants were arranged in special blocks as shown in Table 9 of the Appendix. Data for Stages A, B and C were collected as in Experiment I.

STATISTICAL METHODS

A. Analyses Of Data From The Diallel Crosses

Hayman (1954a, 1954b); Jinks (1954); Jinks and Hayman (1953) developed the analysis for the F_1 generation of a diallel cross. The theory for their method can be divided into 2 parts. The first part proposes a pictorial presentation in which Jinks (1954) stated that "the covariance of array means on the common parent of the array gives the array covariance (W_r)". The W_r values for each array were plotted against the variance of the array (V_r). In order for the basic assumptions for this analysis to be met, these points should lie along a line of unit slope and within a parabola defined as "$W_r^2 = V_r$ x variance of parents". The position of the line gives an estimate of the degree of dominance. When the interception is through the origin, complete dominance is concluded. The interception above or below the origin indicates partial dominance and over-dominance respectively.

The second part proposed a numerical analysis (Table 1) in which the variances and covariances available from the diallel table were defined in terms of the components D, H_1, H_2, F and E (first designated by Mather, 1949), where D was the weighted component of variation due to differences in additive gene effects, H_1 was the weighted components due to dominance, H_2 indicated the asymmetry of positive and negative effects of genes, F was a component due to the relative frequencies of dominant and recessive

TABLE 1. The second degree statistics for a diallel set. (Mather and Jinks, 1971)

Statistics	Model
$\breve{V}_p$	D + E
$\bar{V}_r$	$\frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F + 5/9\ E$
$\bar{W}_r$	$\frac{1}{2}D - \frac{1}{4}F + 1/9\ E$
$V_{\bar{r}}$	$\frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}H_2 - \frac{1}{4}F + 5/81\ E$

$$H_1 = 4\ \bar{V}_r + V_p - 4\ \bar{W}_r - \frac{3n-2}{n} E$$

$$H_2 = 4\ \bar{V}_r - 4V_{\bar{r}} + \frac{2(n^2-1)}{n^2} E$$

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

V_r the variance of an array

W_r parent-offspring covariance of members of the same array

$\bar{W}_r$ mean of W_r

$\bar{V}_r$ mean of V_r

V_p variance of parents

$V_{\bar{r}}$ the variance of array means

E environment effect, derived from the block interactions of the family means (from analysis of variance of diallel table), it has the same value for each block.

D the weighted component of variation due to differences in additive gene effects

H_1 the weighted components due to dominance

H_2 the asymmetry of positive and negative effects of genes

F the relative frequencies of dominant and recessive alleles

alleles, (being positive when dominant alleles are more frequent, and negative when recessive alleles are the more frequent), and E was the component due to environmental error. Additional information may be gained: $D<H_1$, overdominance; $D>H_1$, partial dominance. $F>0$, indicates that the parents carried an excess of dominant over recessive genes, also $(H_1/D)^{\frac{1}{2}}$ indicates the average degree of dominance. If this value is greater than one, there is overdominance; if equal to one, complete dominance; if less than one, partial dominance. Furthermore, $H_2/4H_1$ is an estimate of the average proportion of dominant and recessive alleles over all parental lines. When it is lower than its maximum value of 0.25, the gene frequency of both dominant (u) and recessive (v) genes is not equal at all loci. The function $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ estimates the ratio of the total number of dominant to recessive genes in all parents. The value, h^2/H_2, is an estimate of the number of genes which controls the character and exhibits dominance to some degree. The estimate of the heterozygote value h is calculated as $2(m_{L_1} - m_{L0})$, where m_{L_1} is the mean of all diallel (n^2) progeny and m_{L0} is the mean of diallel (n) parents. The heritability of the trait is calculated as $\frac{1}{4}D/(\frac{1}{4}D+\frac{1}{4}H_1 - \frac{1}{4}F+E)$ (Crumpacker and Allard, 1962).

The theory underlying the partition of the hereditary variance of the diallel crosses into the above components uses 6 assumptions (Hayman, 1954): (1) diploid segregation; (2) no differences between reciprocals; (3) independent action of non-allelic genes; (4) no multiple allelism; (5) homozygous parents; (6) genes independently distributed between the parents.

This method of analysis should only be applied if these

underlying assumptions are met. When the data do not fulfill any of the assumptions there will be a deviation of the W_rV_r regression line from a slope of 1, or an acurvature of the line, or increase scattering of points around the line. When the graphed points give a line of unit slope, the difference between W_r and V_r will be constant. A test of the assumptions in the uniformity of W_r-V_r over arrays and experimental blocks. Lack of uniformity gives no information as to which assumption may have failed, although some ideas can be suggested from the W_rV_r graph.

The methods used and problems attacked by the diallel cross techniques have been diverse. One major system was developed by Jinks and Hayman (1953) who were concerned with gene level as mentioned previously. Another system developed by Griffing (1956) was concerned with gametic level known as general and specific combining ability analysis (G.C.A. and S.C.A. respectively). For the purpose of comparison, both systems of statistical methods were used on the data of this presentation.

The terms general and specific combining ability were originally defined by Sprague and Tatum (1942), but without a generalized genetic interpretation of the combining ability effects. Until 1956, Griffing used a diallel crossing system in quantitative inheritance for the purpose of estimating genetic parameters of the population from which the inbreds were derived. He proposed two assumptions: (1) the situation in which the parental lines simply or the experimental material as a whole are assumed to be a random sample from some population about which inferences may be made (random model), and (2) the situation in which the lines are deliberately chosen and

TABLE 2. Analysis of variance for combining ability giving expectation of mean squares for the assumption of a fixed model.

source of variance	d.f.	sum of squares	mean square	expected mean square
G.C.A.	p-1=2	S_g	M_g	$\sigma^2+2(p-2)[\frac{1}{p-1}]\Sigma g_i^2$
S.C.A.	p(p-1)/2=3	S_s	M_s	$\sigma^2+2[\frac{2}{p(p-3)}]\Sigma\Sigma s_{ij}^2$
Reciprocal effects	p(p-1)/2=3	S_r	M_r	$\sigma^2+2[\frac{2}{p(p-1)}]\Sigma\Sigma r_{ij}^2$
Error	m=27	S_e	M_e	σ^2

where $S_g = \frac{1}{2(p-2)}\Sigma(X_{i.}+X_{.i})^2 - \frac{2}{p(p-2)}X_{..}^2$

$S_s = \frac{1}{2}\Sigma\Sigma_{ij}(X_{ij}+X_{ji})^2 - \frac{1}{2(p-2)}\Sigma(X_{i.}+X_{.i})^2 + \frac{1}{(p-1)(p-2)}X_{..}^2$

$S_r = \frac{1}{2}\Sigma\Sigma_{ij}(X_{ij}-X_{ji})^2$

Testing for overall differences among the various classes of effects can be accomplished as follows:

(1) to test G.C.A. effects use $F_{(p-1),m} = M_g/M_e$

(2) to test S.C.A. effects use $F_{p(p-1)/2,m} = M_s/M_e$

(3) to test for reciprocal effects use $F_{p(p-1)/2,m} = M_r/M_e$

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cannot be regarded as a random sample from any population (fixed model). These two different assumptions give rise to different estimation problems and different tests of hypotheses regarding combining ability effects. In this presentation, only assumption (2) was considered, (Table 2).

The mathematical model for the combining ability analysis is assumed to be: $x_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + 1/b \sum_k e_{ijk}$

where x_{ij} = ith individual of jth parental line

u = overall population mean

g_i (g_j) = the G.C.A. effect for the ith (jth) parent

$i,j = 1,\ldots 3$

s_{ij} = the S.C.A. effect for the cross between the ith and jth parents

r_{ij} = the reciprocal effect involving the reciprocal crosses between the ith and jth parents

e_{ijk} = the environmental effect associated with the ijkth individual observations

b = the number of blocks, $k=1,\ldots 4$

B. Analyses Of Data From Reciprocal Crosses

Some of the data from the greenhouse (Experiment III) and growth chamber (Experiment II) experiments were analyzed partitioning the variance as follows:

The mathematical model for the reciprocal cross analysis is assumed to be: $y_{ij} = u + l_i + b_j + e_{ij}$

where y_{ij} = jth observation in ith line

u = the overall population mean

l_i = an effect due to ith line, $i=1,\ldots 4$

b_j = an effect due to jth block, j=1,...10

e_{ij} = an effect peculiar to jth individual of ith line

Source of variance	d.f.
Block	9
Line	3
Error	27

By the method outlined by Steel and Torrie (1960), the source of line variance was further partitioned into non-orthogonal comparisons as follows:

Line pedigree	B	I	BI	IB
Nucleus	XX	YY	XY	YX
Cytoplasm	P_1	P_2	P_1	P_2
No. of comparisons				
1. B vs. I	+1	-1	0	0
2. BI vs. IB	0	0	+1	-1
3. I vs. IBIB	0	+1	0	-1
4. B vs. BI	+1	0	-1	0

Following is an outline of comparisons tested for significance:

1. B vs. I: the inter-parental comparison
2. BI vs. IB: the F_1 intra-reciprocal comparison. Since the reciprocals have the same nuclear composition, the differences between them will be only due to cytoplasmic effect.

3&4. I vs. IB and B vs. BI: the maternals and their offspring comparisons. Since they have same cytoplasm, the differences will be due to nuclear compositions.

C. Analyses Of Data From Field Experiments

Basically the field experiments were designed with the purpose of determining the extent of variation within each generation, and the selection progress was calculated in the fourth generation. Data from all the field experiments were used to calculate the mean and standard deviation. In the field Experiment II, selection progress (ΔG) and genetic progress (σG) were calculated for both IB and BI populations based on the formulae after Falconer (1967) and Pirchner (1969):

$$G = i\ h\Delta G = i\sigma_p h^2 \quad \& \quad \sigma G = \Delta G/ih$$

where i = selection intensity (1.75)

σ_p = phenotypic variation expressed in standard deviation

h^2 = heritability

The estimate of heritability was calculated using the variance components from the analysis of variance after Robinson et al. (1949); and Grafius et al. (1952).

source variance	d.f.	mean square	expected mean square
Line	r-1	M_1	$\sigma_e^2 + s\sigma_g^2$
Block	s-1	M_2	$\sigma_e^2 + r\sigma_b^2$
Error	(r-1)(s-1)	M_3	σ_e^2

$$h^2 = \sigma_g^2/(\sigma_g^2 + \frac{\sigma_e^2}{s}) = 1 - \frac{M_3}{M_1}$$

(note: h = square root of heritability h^2, and differs from Hayman and Jinks 'h' genetic value of diallel analysis.)

EXPERIMENTAL RESULTS

Diallel Crosses Experiments

The data for the diallel cross experiments show the number of days required for each of the component growth stages as they occurred under the 2 temperature regimes, designated as warm and cool. The data were analyzed by the Jinks and Hayman (1953) and Griffing (1956) methods.

A. Hayman - Jinks Method

(A) Greenhouse Experiment I

This experiment was concerned with the days required for plants to progress through 7 growth component stages in 2 different temperature regimes. The means for the 7 stages in both warm and cool regimes are presented in Table 3. The original data are shown in Tables 10 and 11 of the Appendix.

For each growth stage, diallel tables were set out for each of the four blocks, and W_r and V_r values calculated from them (Table 4); and the means were used to estimate the parameters and estimators. The differences, $W_r - V_r$, were obtained, and their uniformity was tested by analyses of variance.

The uniformity test of $W_r - V_r$ for each of the characteristics in Experiment I revealed that only Stage 3 in warm, and Stage 6 in cool showed significant differences among arrays (Table 5), indicating that these 2 characteristics lack uniformity. The analyses gave no information as to which of the assumptions may have failed. It was

TABLE 3. Mean number of days required for each of the 7 stages in the diallel cross tested in warm and cool temperature regimes in greenhouse Experiment I.

Male† parent	Stage	Female parent†					
		B		I		C	
		Temperature					
		warm	cool	warm	cool	warm	cool
B	1	8.7	18.5	6.5	15.9	6.9	14.8
	2	9.2	9.5	8.5	8.4	11.0	10.6
	3	32.6	36.7	22.4	23.4	20.2	28.6
	4	21.8	70.8	21.3	59.3	17.8	52.8
	5	9.0	22.9	6.4	17.0	7.2	18.1
	6	44.8	63.9	37.7	45.0	44.2	64.6
	7	6.8	7.8	5.2	6.8	5.3	7.3
I	1	7.0	5.1	7.3	16.3	6.3	15.7
	2	9.1	8.6	9.0	9.5	10.0	10.8
	3	21.5	23.3	17.3	20.1	18.5	19.2
	4	27.3	51.3	18.5	58.0	17.8	47.5
	5	6.0	8.8	6.5	20.0	6.7	18.8
	6	40.7	42.4	35.9	48.9	39.8	58.1
	7	5.1	7.6	5.0	7.5	5.0	9.6
C	1	7.2	16.4	6.4	15.8	7.4	15.8
	2	8.7	8.9	10.2	11.2	9.2	12.4
	3	21.8	76.1	18.8	18.8	22.1	26.7
	4	20.8	52.8	17.0	59.3	22.8	51.8
	5	28.0	18.0	6.2	17.9	7.4	18.3
	6	45.9	64.8	39.8	58.8	48.1	53.0
	7	5.6	7.1	5.0	8.8	6.4	8.3

† B, Bonny Best
I, Immur Prior Beta
C, Cold Set

TABLE 4. Calculated mean values of V_r and W_r for the 7 stages in the diallel cross tested in warm and cool regimes in greenhouse Experiment I.

Array	Stage	V_r		W_r		W_r-V_r		W_r+V_r	
		Temperature							
		warm	cool	warm	cool	warm	cool	warm	cool
B†	1	1.5	3.8	0.9	2.6	-0.6	-1.2	2.4	6.4
	2	0.5	0.7	0.1	0.7	-0.4	0.0	0.6	1.4
	3	42.4	48.5	47.2	55.6	4.8	7.1	89.6	104.1
	4	4.9	95.8	1.9	92.5	-3.0	-3.3	6.8	188.3
	5	2.0	7.9	1.8	6.2	-0.2	-1.7	3.8	14.1
	6	11.4	142.5	20.1	63.8	8.7	-78.7	31.5	206.3
	7	0.8	2.4	0.9	1.7	-0.1	-0.7	1.7	4.1
I	1	0.3	2.7	-0.1	-0.6	-0.4	-1.3	0.2	0.1
	2	0.6	1.6	0.1	1.9	-0.5	0.3	0.7	3.5
	3	6.5	5.8	18.9	5.9	12.4	0.1	25.4	21.7
	4	2.8	7.1	0.1	4.8	-2.7	-2.3	2.9	11.9
	5	0.1	1.2	-0.1	-0.5	-0.2	-1.7	0.1	0.7
	6	5.6	55.8	14.5	-33.4	-8.9	-89.2	20.1	22.4
	7	0.1	4.1	0.1	-0.3	0.0	-4.4	0.2	3.8
C	1	0.4	0.3	0.2	-0.1	-0.2	-0.4	0.6	0.2
	2	0.3	2.0	-0.1	2.0	-0.4	0.0	0.2	4.0
	3	4.6	22.8	7.5	33.1	2.9	10.3	12.1	55.9
	4	7.9	2.0	6.5	4.6	-1.4	2.6	14.4	6.6
	5	0.8	0.2	1.0	-0.4	0.2	-0.6	1.8	0.2
	6	18.4	44.7	29.8	33.7	11.4	-10.0	48.2	78.4
	7	0.1	0.8	0.1	-1.0	0.0	-1.8	0.2	-0.2

† see Table 3 notation

TABLE 5. Uniformity test of W_r-V_r values by analyses of variance for all the characters investigated in the diallel cross experiments.

Trait		mean square
Stage 1 in warm		0.02
2		0.02
3		85.67*
4		0.63
5		0.33
6		0.05
7		0.01
Stage 1 in cool		1.10
2		0.10
3		3.43
4		40.85
5		1.86
6		927.59*
7		1.33
days required per plastochron in warm		0.02
days required per plastochron in cool		0.01
days required for Stage (pollination treatment)	5 in warm	0.17
	6 in warm	3.45
days required for stage (pollination treatment)	5 in cool	0.21
	6 in cool	18.39
fruit weight in warm		6477.58
fruit diameter in warm		353.10
fruit weight in cool		17016.20*
fruit diameter in cool		72.57

* significant at the 5% level

recognized that sample error could have produced these significant results. Nevertheless, it was advisable to proceed with the total analysis; however, some caution should be attached to interpretation of results.

(a) Graphical Interpretation of the Genetic Parameters

The regressions of W_r on V_r are shown in Fig. 1-4 and provides the following information.

Stage 1, warm: The regression coefficient was 1.005 which was not significantly different from one. This showed a low level of epistatic gene action. Since the line of unit slope moved downward from origin to the right, then overdominance is suggested. Jinks (1954) and Hayman (1954) indicated that the positions of the array points along the line of regression of W_r on V_r depend on the relative proportion of dominant and recessive alleles present in the common parent of each array. Parents with a preponderance of dominant alleles will have a low array variance and covariance, and will lie near the origin. On the other hand, parents with recessive alleles will have a large array variance and covariance, and will lie at the opposite end of the regression line. Fig. 1 indicated that the B parent had relatively low, and C and I had relatively high levels of dominance

Hayman (1954) stated that:

> "A measure of association between the signs of dominant genes is the correlation between parental size and parental order of dominance. The parental measurement, (y_r), is closely correlated with the number of positive homozygotes in the parent while (W_r+V_r) bears the same relation to the number of recessive homozygotes."

When the correlation between y_r and (W_r+V_r) is nearly one, the recessive genes must be mostly positive; when the correlation is minus

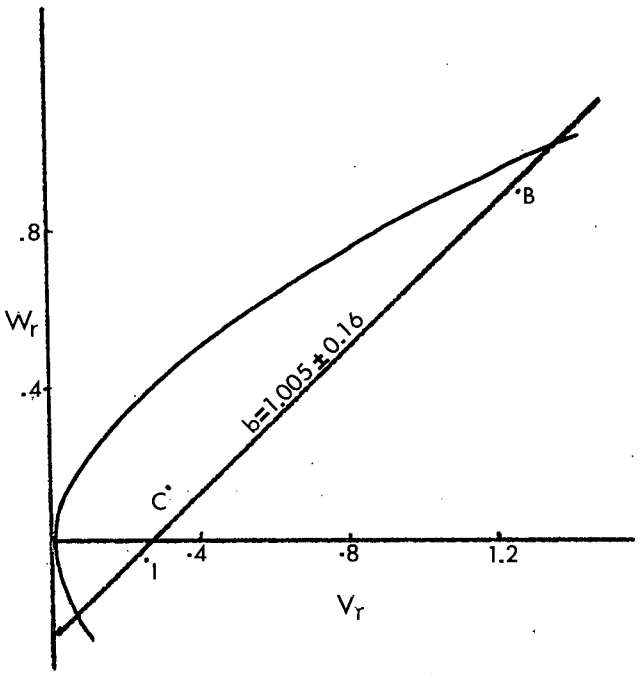

Fig. 1. (V_r,W_r) graph for Stage 1, greenhouse Experiment I, warm regime.

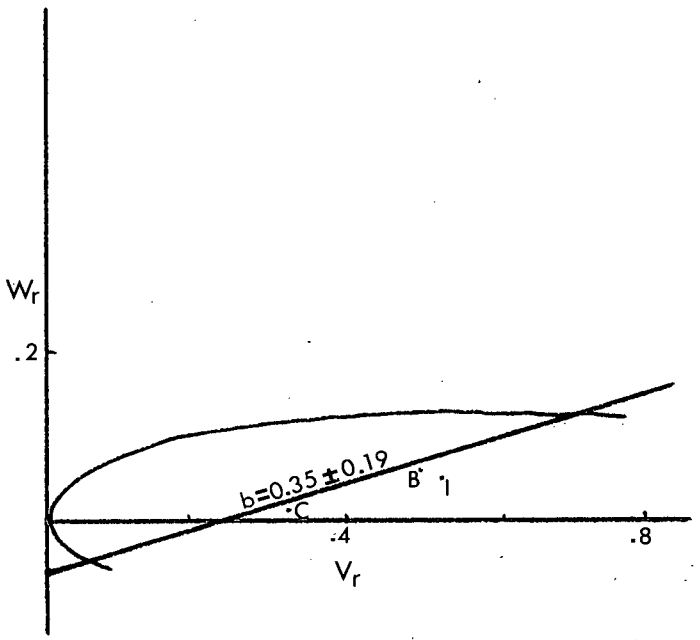

Fig. 2. (V_r,W_r) graph for Stage 2, greenhouse Experiment I, warm regime.

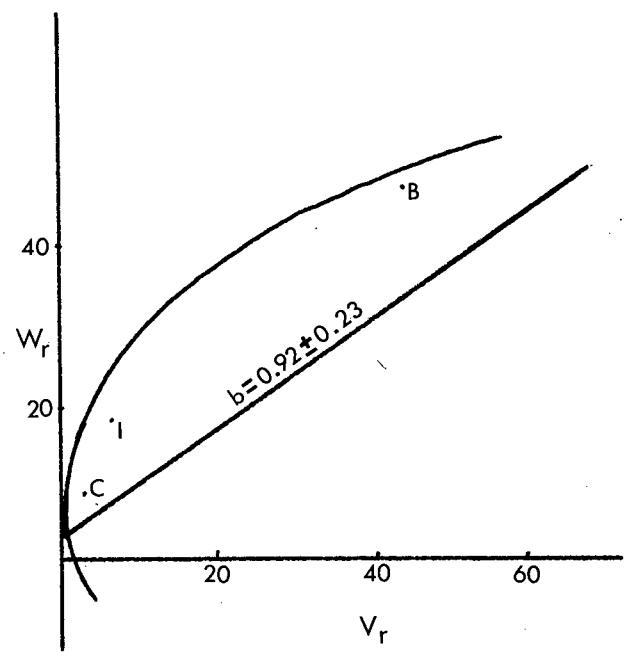

Fig. 3. (V_r,W_r) graph for Stage 3, greenhouse Experiment I, warm regime.

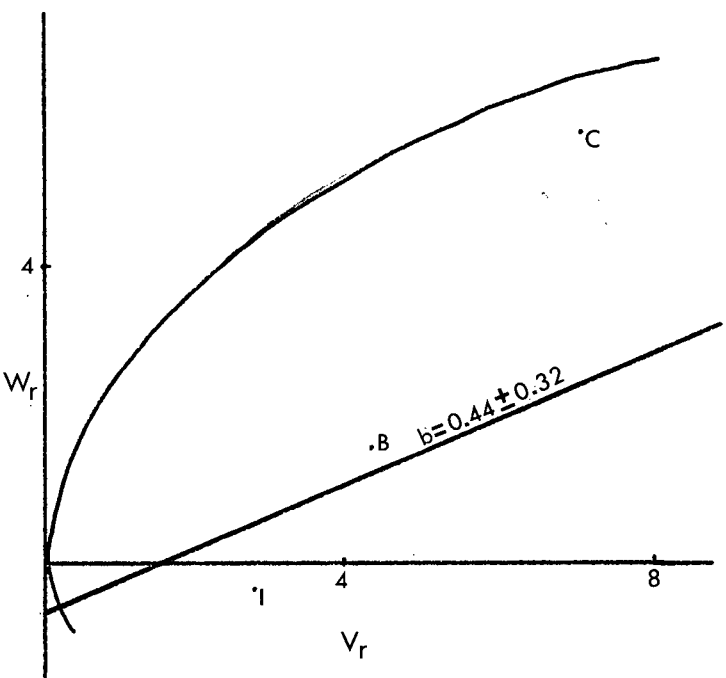

Fig. 4. (V_r,W_r) graph for Stage 4, greenhouse Experiment I, warm regime.

one, the dominant genes are positive; when the correlation is small, equal proportions of the dominant genes are positive and negative in their effects. As shown in Table 6, this correlation between y_r and $W_r + V_r$ for Stage 1 warm was 0.99, and indicates that most of the recessive alleles in the parents are acting in the direction of lateness and the dominant alleles in the direction of earliness.

Stage 2, warm: The regression coefficient was 0.35 which was significantly different from both one and zero (Fig. 2). This value indicates that both dominant and additive genes must be operating. Since W_r is related to V_r by a straight regression line, it could be concluded that epistatic gene action was minimal; and since the regression line cuts the W_r axis downward from the origin, overdominance was suggested. Although the positions of the array points B, I and C were close together, C is closer to the point of origin indicating dominance over B and I. The correlation between y_r and $W_r + V_r$ is negative (Table 6), but the relatively small value of -0.19 indicates practically equal proportions of the dominant genes contribute to earliness (negative) or lateness (positive).

Stage 3, warm: As indicated before (Table 5) the analysis of variance for $W_r - V_r$ failed to prove uniformity among arrays, indicating that one of the assumptions may not have been met; however, some idea of gene action may be gained from the $W_r V_r$ graph (Fig. 3). The regression coefficient was 0.92 which is not significantly different from one and thus shows absence of appreciable epistatic gene action. The line of unit slope cuts the W_r axis upwards from the origin and thus indicates that partial dominance is functioning. From the graph, it may be concluded that B was acting recessively and I and C dominantly.

TABLE 6. Correlation coefficient between parental values (y_r) and W_r+V_r for all characters investigated in the diallel cross experiments.

Traits	correlation coefficient
Stage 1 in warm	0.99
2	-0.19
3	0.86
4	0.85
5	0.96
6	0.82
7	0.97
Stage 1 in cool	0.93
2	0.49
3	0.98
4	0.94
5	0.96
6	0.99
7	0.78
days required per plastochron in warm	0.52
days required per plastochron in cool	0.93
days required for Stage 5 in warm (pollution treatment)	0.84
6 in warm	0.79
days required for Stage 5 in cool (pollution treatment)	0.79
6 in cool	0.80
fruit weight in warm	0.92
fruit diameter in warm	0.53
fruit weight in cool	0.97
fruit diameter in cool	0.83

The correlation coefficient between y_r and W_r+V_r was 0.86 and because it was positive and relatively close to one, it appears that the recessive alleles in the parents are acting in the direction of lateness and the dominant alleles in the direction of earliness.

Stage 4, warm: The regression coefficient was 0.44 (Fig. 4) and was significantly different from both one and zero, which indicated that both dominant and additive genes were functioning. Since W_r is related to V_r by a straight regression line, it could be concluded that non-allelic gene interaction was absent, and since the regression line was downward right from the origin, then overdominance must be present. The positions of array points for B, I and C indicate intermediate, high and low levels of dominance respectively. The correlation between y_r and W_r+V_r was 0.85 which was positive and high, hence providing evidence that recessive alleles are acting in the direction of lateness and the dominant alleles in the opposite direction.

Stage 5, warm: The regression coefficient was 0.94 (Fig. 5) which was not significantly different from one, and indicated absence of epistatic gene action. The line of unit slope which almost goes through the origin, indicated practically complete dominance. The array points show that B,C and I were acting at relatively low, intermediate and high levels of dominance respectively. The correlation between y_r and W_r+V_r was 0.96 which was positive and high, and provides evidence that the recessive alleles in the parents were acting in the direction of lateness.

Stage 6, warm: The regression coefficient was 0.98 (Fig. 6) which was not significantly different from one; therefore, absence of epistatic gene action was expected. The line of unit slope which is

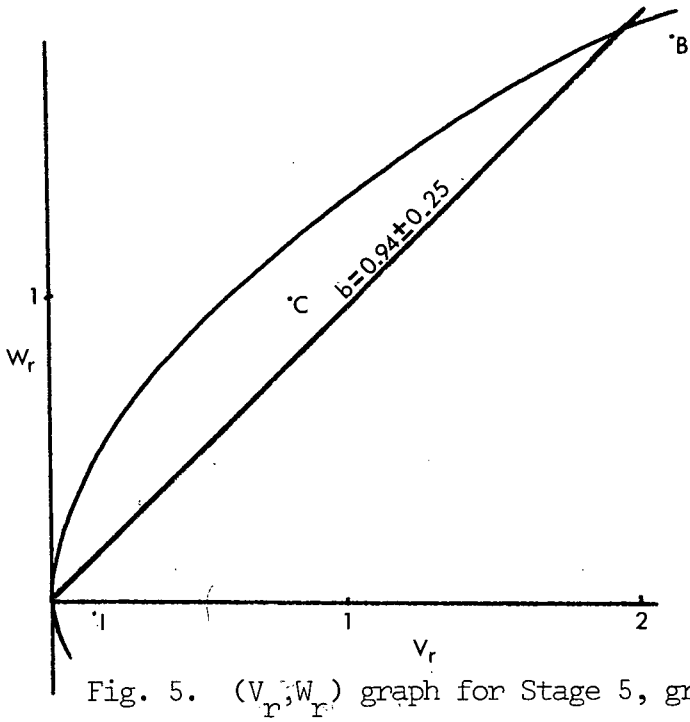

Fig. 5. (V_r, W_r) graph for Stage 5, greenhouse Experiment I, warm regime.

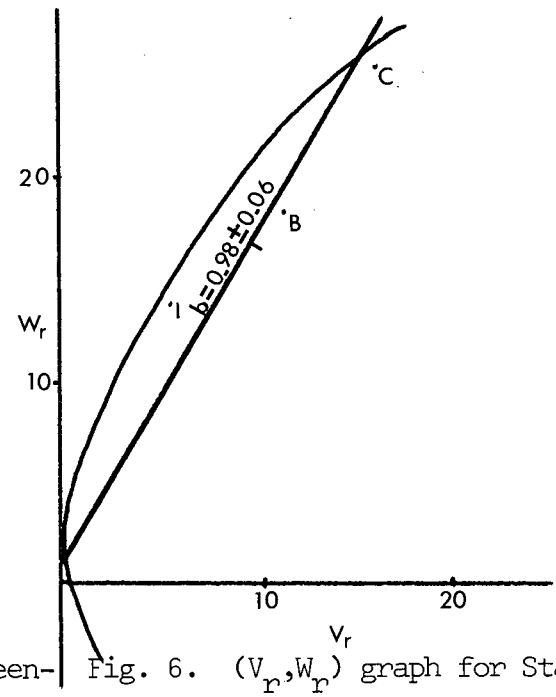

Fig. 6. (V_r, W_r) graph for Stage 6, greenhouse Experiment I, warm regime.

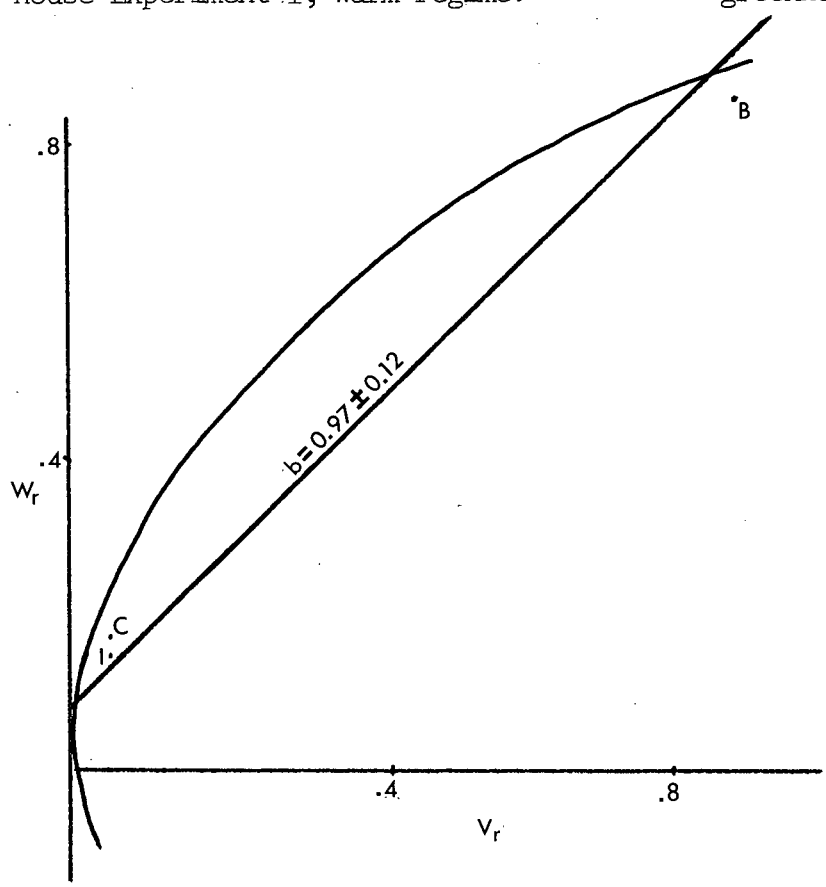

Fig. 7. (V_r, W_r) graph for Stage 7, greenhouse Experiment I warm regime.

very close to the point of origin indicated partial to complete dominance. The position of the array points indicated that there was a sequence of C, B and I which ranged from low to high levels of dominance. The correlation coefficient between y_r and W_r+V_r was 0.82 which provides evidence that recessive genes were acting in the direction of lateness.

Stage 7, warm: The regression coefficient was 0.97 (Fig. 7) which was not significantly different from unity which indicated an absence of epistatic gene action. The regression line cut the W_r axis upward left from the origin and indicated partially dominant gene action. The position of the array points showed that C and I had a relatively high level of dominance compared with the low level for B. The correlation between y_r and W_r+V_r was 0.97, again provided evidence that most of the recessive alleles in the parents must have been acting in the direction of lateness.

Stage 1, cool: The regression coefficient was 0.71 (Fig. 8) which was not significantly different from one. This line showed the same gene action and sequence of dominance as Stage 1 in warm conditions. Similarly the correlation coefficient of 0.93 was essentially the same as for Stage 1, warm.

Stage 2, cool: The regression coefficient was 0.87 (Fig. 9) which was not significantly different from one, indicating absence of epistatic gene action. The regression line cuts the W_r axis, left and upward from the origin, indicating partial dominance. The level of dominance for the parents ranged from low to high in the order of C, I and B. It was noted that for the first time B showed the highest level of dominance. The correlation between y_r and W_r+V_r was

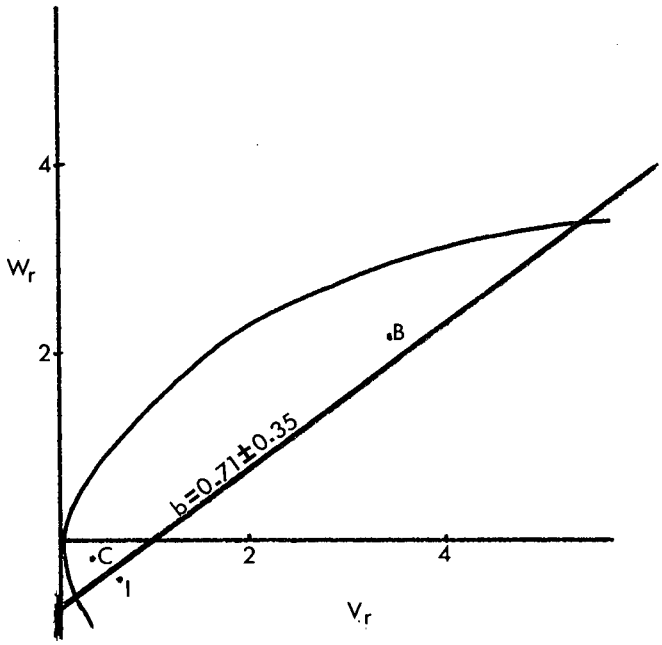

Fig. 8. (V_r,W_r) graph for Stage 1, greenhouse Experiment I, cool regime.

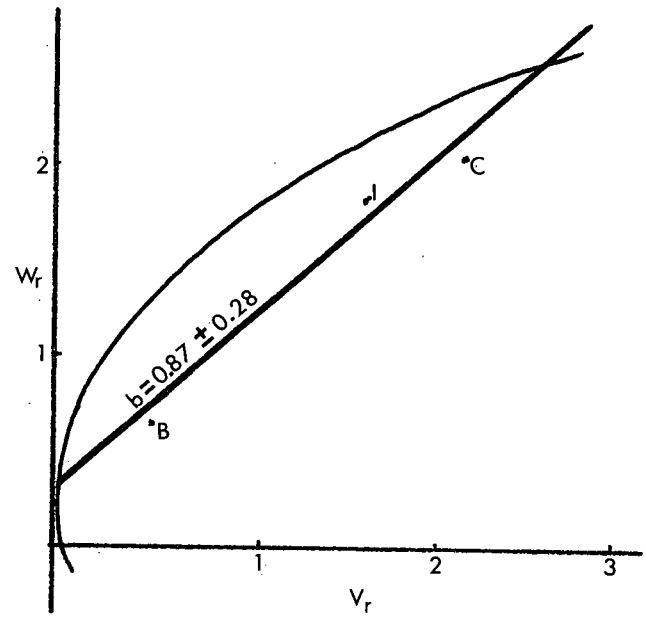

Fig. 9. (V_r,W_r) graph for Stage 2, greenhouse Experiment I, cool regime.

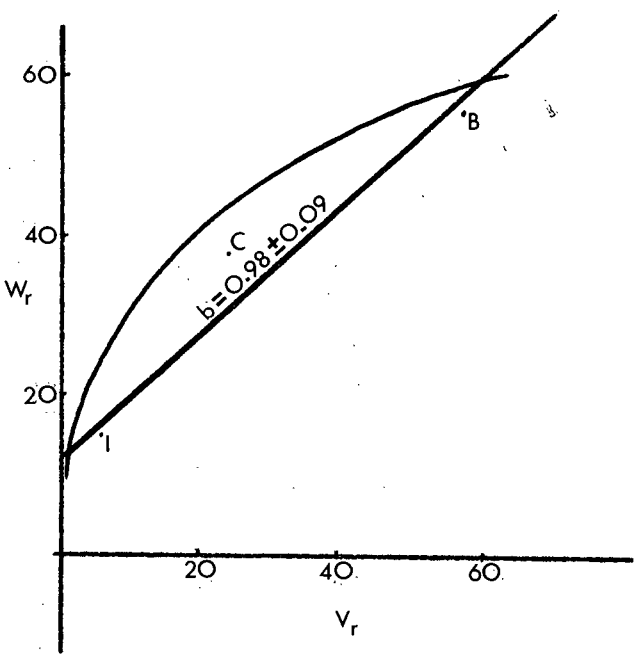

Fig. 10. (V_r,W_r) graph for Stage 3, greenhouse Experiment I, cool regime.

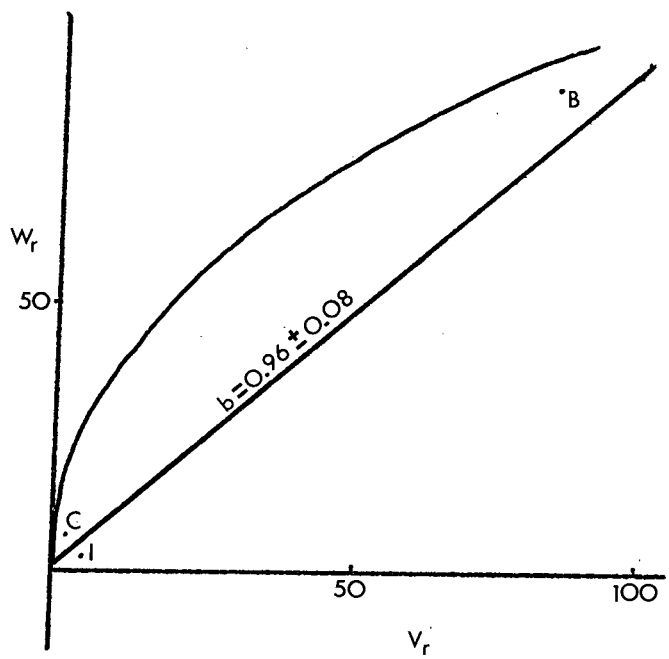

Fig. 11. (V_r,W_r) graph for Stage 4, greenhouse Experiment I, cool regime.

0.49 which was small, indicating there were equal proportions of the dominant genes which were positive or negative. In other words, the dominant genes did not work entirely in the direction of earliness, but about one half must have been contributing to lateness.

Stage 3, cool: The regression coefficient was 0.98 (Fig. 10) indicating the same gene action as above for Stage 2 in cool. The sequence for the level of dominance from low to high was B, C and I. The correlation coefficient between y_r and W_r+V_r was 0.98 indicating the recessive genes were acting in the direction of lateness.

Stage 4, cool: The regression coefficient between W_r and V_r was 0.96 (Fig. 11) which was the same as that for Stage 5, warm. Thus there was no appreciable epistatic gene action, but complete dominance was indicated. The graph shows that B had a very low level of dominance whereas C and I had a very high level. In other words, C and I will be acting as dominant over B. The correlation coefficient between y_r and W_r+V_r was 0.94, which was high and positive indicating that dominant gene action was in the direction of earliness.

Stage 5, cool: The regression coefficient between W_r and V_r was 0.89 (Fig. 12) and suggested the same gene action as for Stage 1, cool. The correlation coefficient between y_r and W_r+V_r was 0.96 indicating that the recessive genes were acting in the direction of lateness.

Stage 6, cool: As in the case of Stage 3 in warm, the analysis of variance failed to prove the uniformity of W_r-V_r over arrays in Stage 6 in cool. Thus one of the assumptions for this diallel cross theory did not fit. Nevertheless, some idea may still be gained from the W_rV_r graph (Fig. 13). The regression coefficient between W_r and V_r

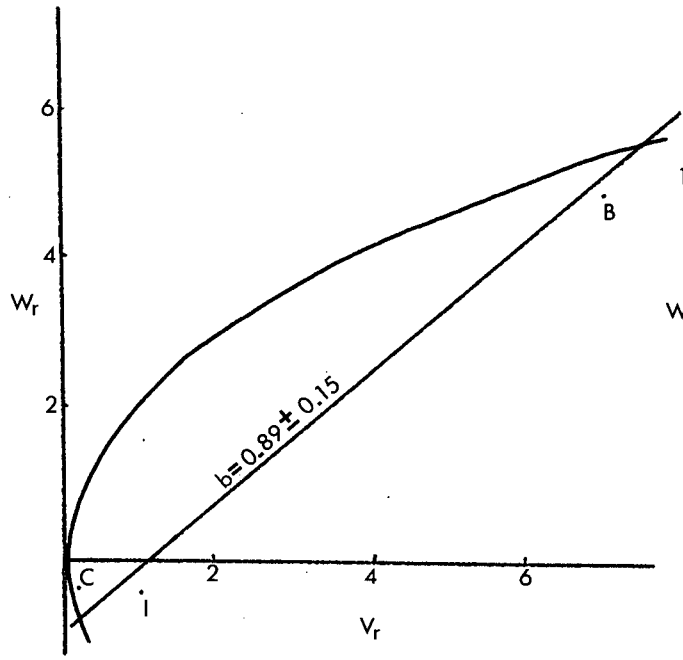

Fig. 12. (V_r,W_r) graph for Stage 5, greenhouse Experiment I, cool regime.

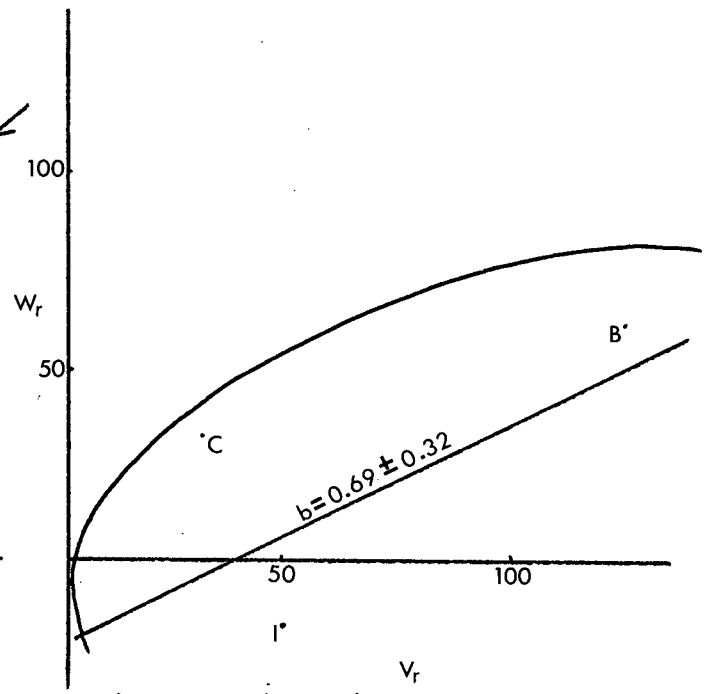

Fig. 13. (V_r,W_r) graph for Stage 6, greenhouse Experiment I, cool regime.

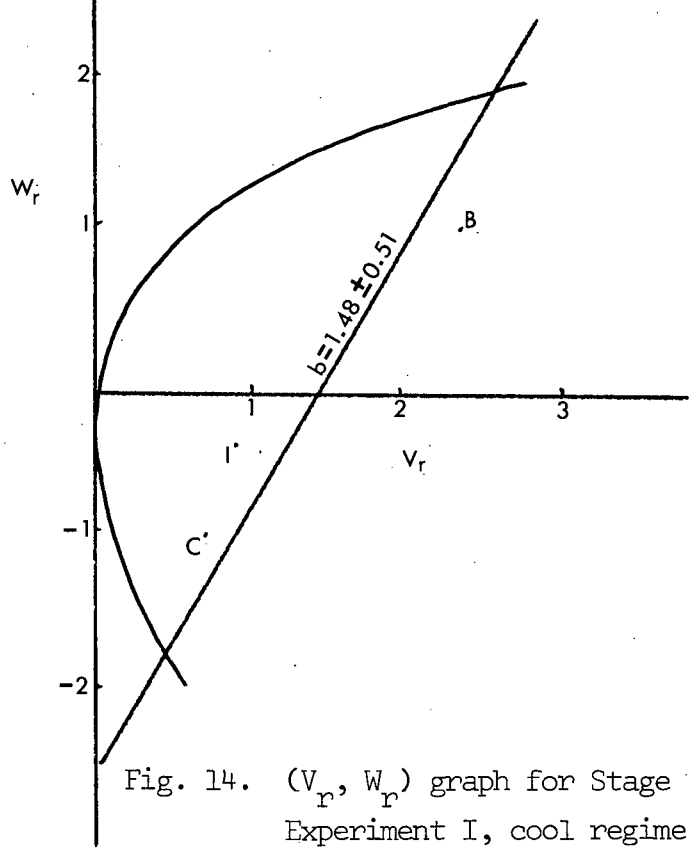

Fig. 14. (V_r, W_r) graph for Stage 7, greenhouse Experiment I, cool regime.

was 0.69 which was significantly different from one. This coefficient indicated that some epistatic gene action and additive gene action may be present. It can be seen that C and I were relatively dominant over B. The correlation coefficient between y_r and W_r+V_r was 0.99 indicating that the recessive genes were acting in the direction of lateness.

Stage 7, cool: The regression coefficient between W_r and V_r was 1.48 (Fig. 14) which was not significantly different from one, indicating the same gene action as Stages 1 and 5 in cool. The correlation coefficient was 0.78 from which it may be concluded that the recessive genes were acting in the direction of lateness but may be acting ambidirectionally.

(B) Greenhouse Experiment II

This experiment was mainly concerned with Stages 5 and 6, and to ensure fruit set potential, pollen was transferred by hand within the same cultivar. The mean values for both warm and cool regimes are presented in Table 7. The original data are shown in Tables 9 and 10 of the Appendix. The design and analysis were the same as for Experiment I, but the management employed artificial pollination to ensure a uniformity of first days, i.e. beginning of Stage 5. Table 7 needs the comparison of the controlled pollination with the natural pollination treatment employed in Experiment I (Table 3).

The calculated W_r and V_r values are shown in Table 8, the pictorial regression lines in Figs. 15, 16, 17 and 18. The genetic information was essentially the same as Experiment I, in other words, although these two experiments differed in pollination methods, the gene action was similar.

TABLE 7. Mean number of days required for Stages 5 and 6 in the diallel cross tested in warm and cool regimes in greenhouse Experiment II.

Male † parent	Stage	Female parent† B		I		C	
		Temperature					
		warm	cool	warm	cool	warm	cool
B	5	8.0	6.6	6.3	7.9	6.8	7.9
	6	40.0	58.6	35.3	53.8	42.5	62.9
I	5	6.1	7.5	6.3	9.3	6.5	8.6
	6	35.5	54.3	31.5	52.5	36.4	55.4
C	5	8.0	7.6	6.5	10.0	6.1	7.5
	6	38.8	64.9	37.0	58.3	43.2	57.8

† see Table 3 notation

TABLE 8. Calculated mean values of V_r and W_r for Stages 5 and 6 in the diallel cross tested in warm and cool regimes in greenhouse Experiment II.

Array	Stage	V_r		W_r		W_r-V_r		W_r+V_r	
		Temperature							
		warm	cool	warm	cool	warm	cool	warm	cool
B†	5	0.9	0.5	0.8	0.6	-0.1	0.1	1.7	1.1
	6	11.8	32.2	21.1	14.3	9.3	-17.9	32.9	46.5
I	5	0.3	1.2	0.1	0.9	-0.2	-0.3	0.4	2.1
	6	10.9	7.8	20.6	5.6	0.7	-2.2	31.5	13.4
C	5	0.5	1.5	0.7	1.2	0.2	0.3	1.2	2.7
	6	12.3	16.1	17.6	9.7	5.3	-6.4	29.9	25.8

† see Table 3 notation

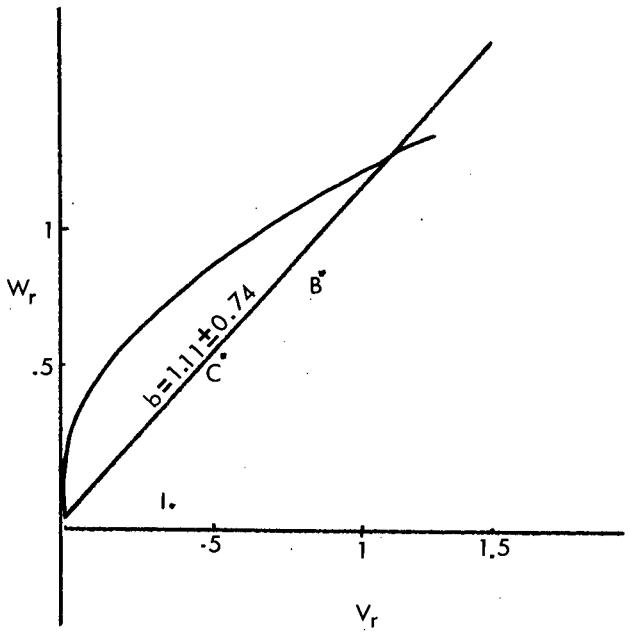

Fig. 15. (V_r,W_r) graph for Stage 5, greenhouse Experiment II, warm regime.

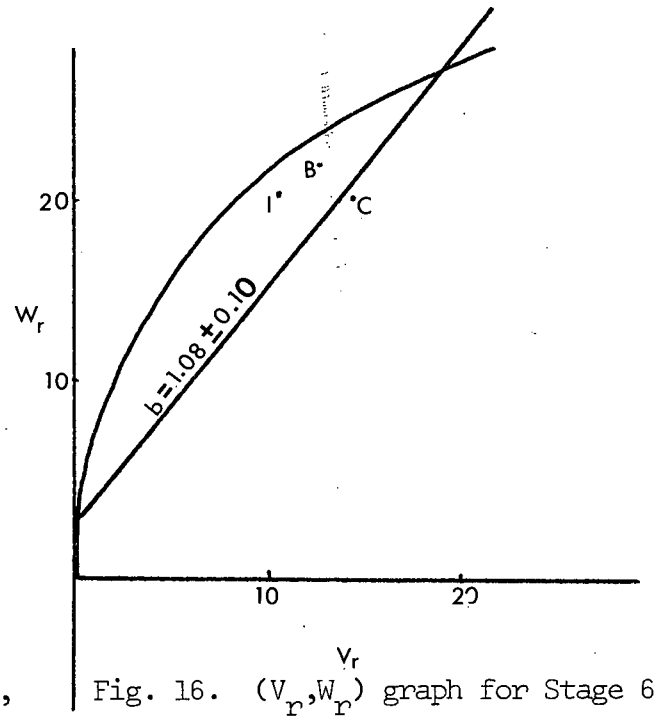

Fig. 16. (V_r,W_r) graph for Stage 6, greenhouse Experiment II, warm regime.

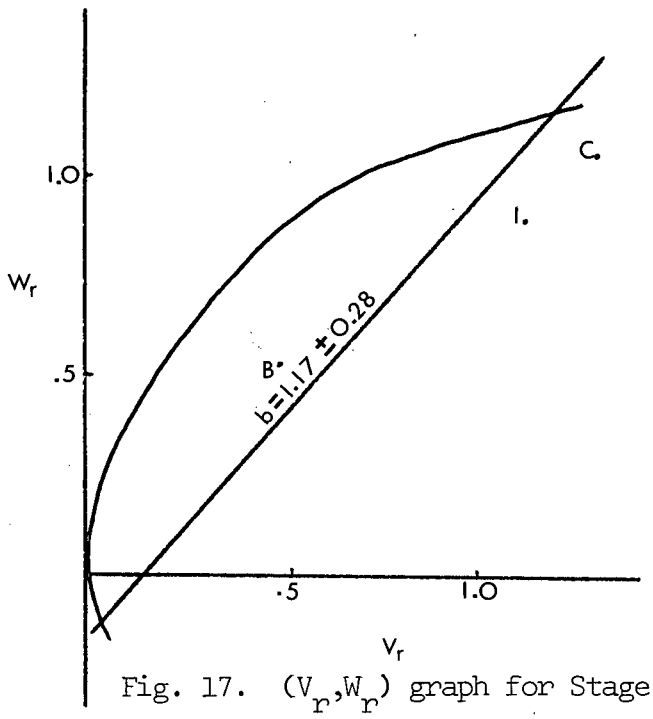

Fig. 17. (V_r,W_r) graph for Stage 5, greenhouse Experiment II, cool regime.

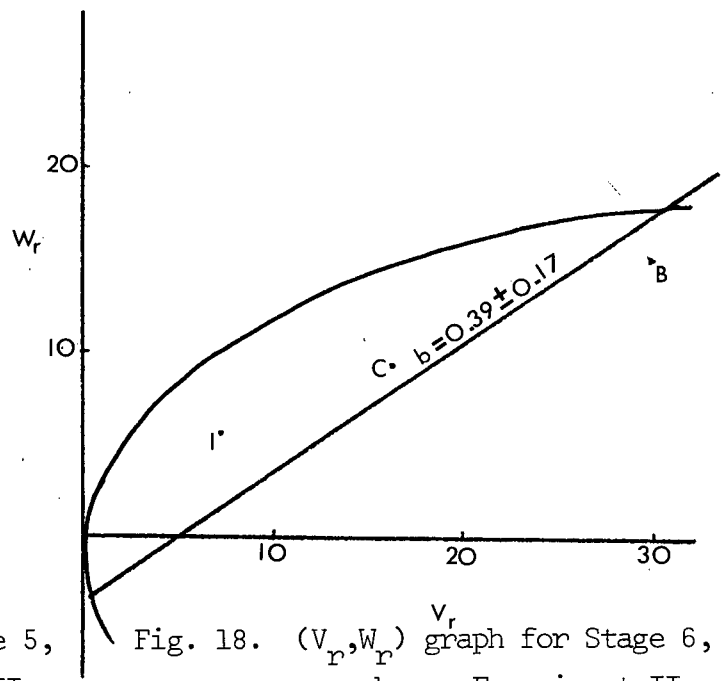

Fig. 18. (V_r,W_r) graph for Stage 6, greenhouse Experiment II, cool regime.

Days Required per Plastochron, warm: Days required per plastochron in both temperature regimes were measured from the 3rd to 8th plastochron (Table 9, plus Tables 11 and 12 of the Appendix). There was no significant differences among arrays for the W_r-V_r uniformity test (Table 5). The regression coefficient between W_r and V_r was 0.81 (Fig. 19) which was not significantly different from one, indicating the absence of epistatic gene action. The regression line cut the origin of the axis meaning that there was complete dominance. The sequence for the level of dominance for the parents was C, B and I from low to high. The correlation coefficient between y_r and W_r+V_r was 0.52 (Table 5) which was small, indicating equal proportions of the dominant genes were positive and negative.

Days Required per Plastochron, cool: The regression coefficient between W_r and V_r for the days required per plastochron in the cool regime was 0.91 (Fig. 20), which was not significantly different from one, indicating the absence of epistatic gene action. The regression line cut the W_r axis downward from the origin meaning that there was overdominance. The sequence for the level of dominance from low to high was C, I and B. The correlation coefficient between y_r and W_r+V_r was 0.93 (Table 6), which was positive and high indicating that the recessive genes were working in the direction of more days required per plastochron (lateness).

Fruit Weight and Fruit Diameter in Both Regimes: The mean values for both temperature regimes are presented in Table 11 and the original data are shown in Table 13 of the Appendix. The uniformity test showed a similar trend for the value of W_r-V_r between arrays (Table 5), indicating the assumptions of the theory were met in the

TABLE 9. Mean number of days required per plastochron in the diallel cross tested in warm and cool regimes in greenhouse Experiment II.

Male parent†	Female parent†					
	B		I		C	
	Temperature					
	warm	cool	warm	cool	warm	cool
B	4.4	6.0	3.7	5.9	4.1	5.4
I	3.6	5.3	3.7	5.9	4.1	5.7
C	3.8	5.9	3.9	5.7	4.1	6.3

† see Table 3 notation

TABLE 10. Calculated mean values of V_r and W_r for the days required per plastochron in the diallel cross tested in warm and cool regimes in greenhouse Experiment II.

Array	V_r		W_r		W_r-V_r		W_r+V_r	
	Temperature							
	warm	cool	warm	cool	warm	cool	warm	cool
B†	0.13	0.05	0.12	0.04	-0.01	-0.01	0.25	0.09
I	0.12	0.05	0.01	0.03	-0.11	-0.02	0.13	0.08
C	0.21	0.14	0.17	0.08	-0.04	-0.06	0.38	0.22

† see Table 3 notation

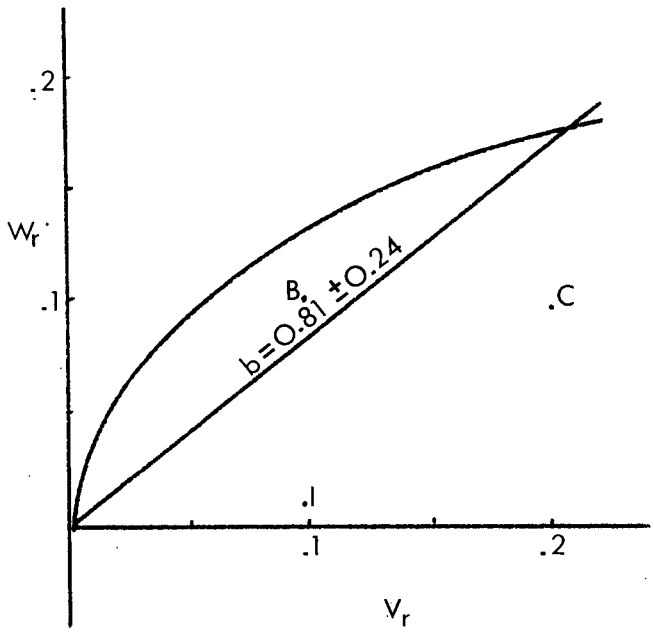

Fig. 19. (V_r,W_r) graph for days required per plastochron, greenhouse Experiment II, warm regime.

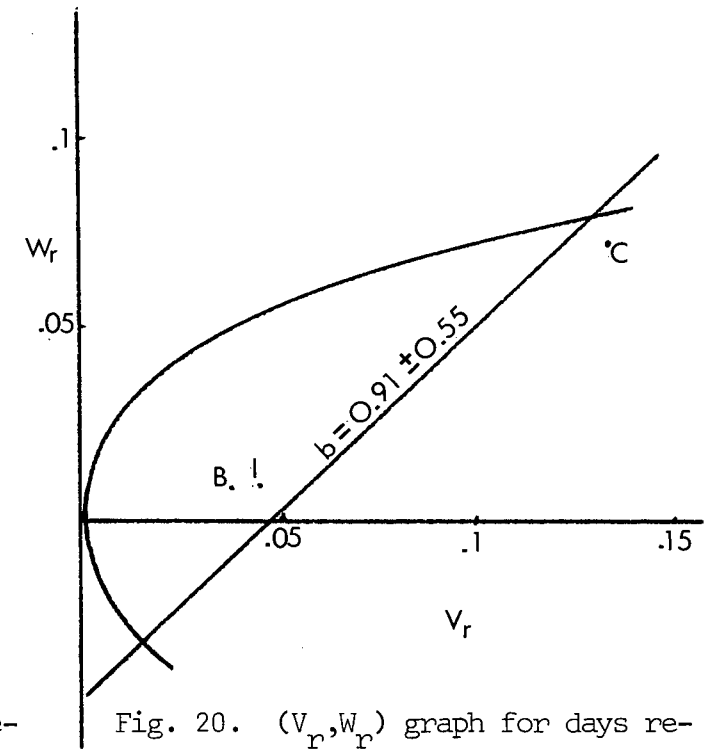

Fig. 20. (V_r,W_r) graph for days required per plastochron, greenhouse Experiment II, cool regime.

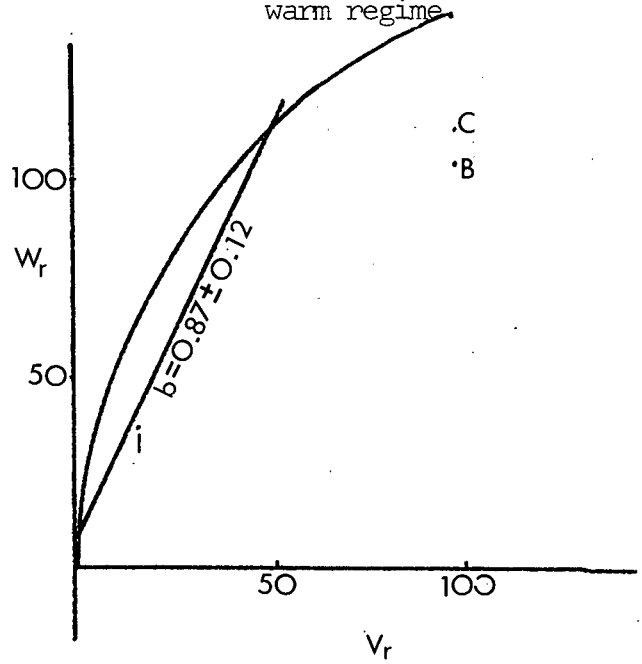

Fig. 21. (V_r,W_r) graph for fruit weight, greenhouse Experiment II, warm regime.

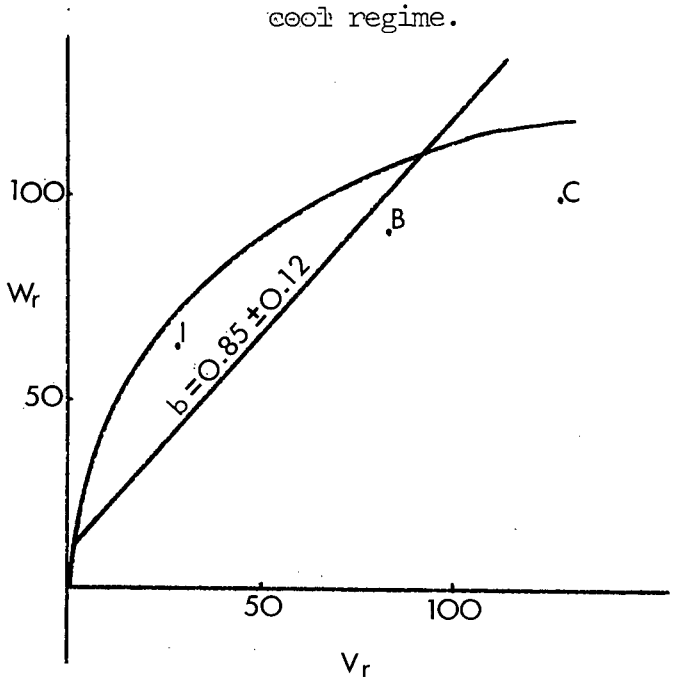

Fig. 22. (V_r,W_r) graph for fruit diameter, greenhouse Experiment II, warm regime.

TABLE 11. Mean fruit weight (g) and fruit diameter (mm) in the diallel cross tested in warm and cool regimes in greenhouse Experiment II.

Male parent	Trait	Female parent					
		B		I		C	
		Temperature					
		warm	cool	warm	cool	warm	cool
B	di.†	55.9	73.0	41.0	48.9	54.3	55.8
	wt.†	92.8	202.5	37.7	62.5	80.3	98.4
I	di.	42.0	45.5	33.9	37.5	42.4	47.8
	wt.	39.0	52.4	21.2	28.5	40.5	55.3
C	di.	57.1	56.3	40.5	46.1	52.1	52.9
	wt.	99.6	91.5	37.8	51.5	76.8	76.9

† di.† = fruit diameter
† wt.† = fruit weight

TABLE 12. Calculated mean values of V_r and W_r for the fruit weight and fruit diameter in the diallel cross tested in warm and cool regimes in greenhouse Experiment II.

Array	Trait	V_r		W_r		W_r-V_r		W_r+V_r	
		Temperature							
		warm	cool	warm	cool	warm	cool	warm	cool
B	di.†	79.3	179.8	91.9	238.8	12.6	59.0	171.2	418.6
	wt.†	1015.6	5767.4	1061.2	6810.9	46.4	1043.5	2076.8	12578.3
I	di.	29.2	34.7	57.8	85.3	28.6	50.6	87.0	120.0
	wt.	138.6	272.7	426.9	1080.9	288.3	808.2	565.5	1353.6
C	di.	73.6	24.8	98.8	79.1	25.2	54.3	172.4	103.9
	wt.	1009.0	453.3	1242.5	1745.8	233.5	1292.5	2251.5	2199.1

† di. = fruit diameter
† wt. = fruit weight

present experiment for both fruit weight and diameter in both the temperature regimes except the case of fruit weight in cool which failed the uniformity test. The fruit weight in warm had a regression coefficient of 0.87 (Fig. 21) which was not significantly different from one, indicating the absence of epistatic gene action. The regression line cut the W_r axis upward from the origin pointing to partial dominant gene action. The sequence for the level of dominance is C, B and I from low to high, meaning I cultivar is dominant over the C and B. The oorrelation coefficient between y_r and W_r+V_r was 0.92, which was positive and high, meaning the recessive genes operated in the direction of heavier fruit weight.

Fruit diameter in warm had a regression coefficient of 0.85 (Fig. 22) which was not significantly different from one and hence the same gene action as that for the fruit weight in warm. The correlation coefficient was 0.53 which was positive but not very high, indicating that almost equal proportions of the dominant genes were positive or negative. Regarding fruit weight in cool, although the differences between arrays for W_r-V_r failed to meet the uniformity test, nevertheless some genetic information may be gained from examining Fig. 23, and noting that gene action was apparently similar to that for fruit weight in warm. The only difference from warm regime results was the sequence for the level of dominance from low to high among the parents which was B, C and I rather than C, B and I as in the warm regime. The correlation coefficient between y_r and W_r+V_r was 0.97, which was positive and high thus indicating that recessive genes were functioning in the direction of heavier fruit weight.

Fruit diameter in cool had a regression coefficient of 1.04

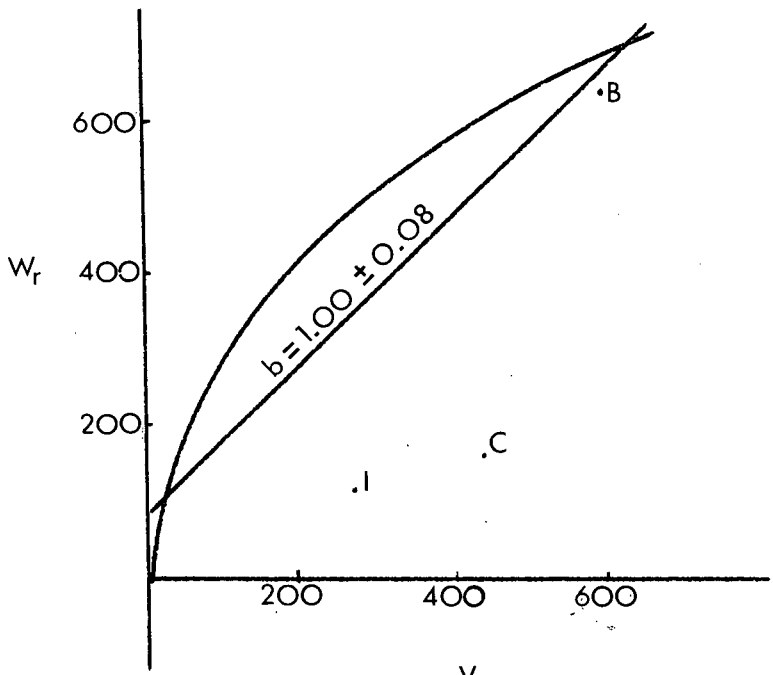

Fig. 23. (V_r,W_r) graph for fruit weight, greenhouse Experiment II, cool regime.

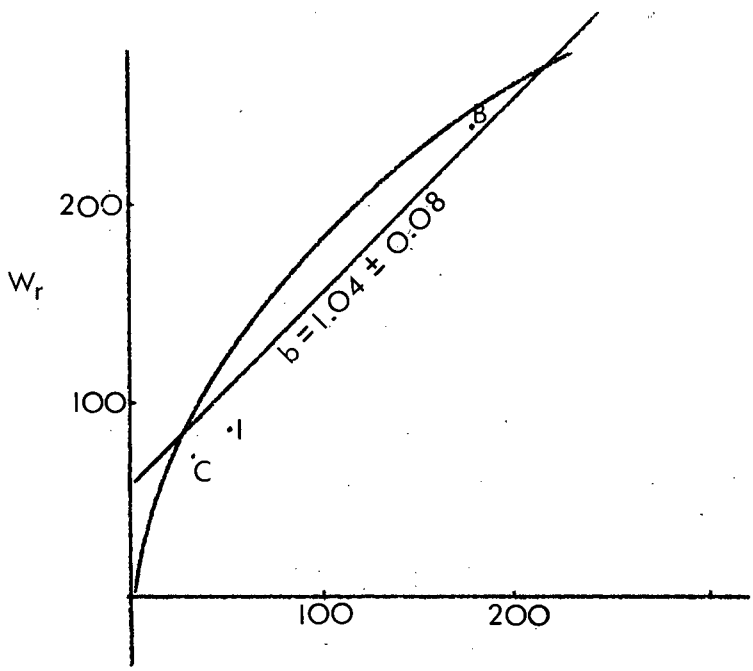

Fig. 24. (V_r,W_r) graph for fruit diameter, greenhouse Experiment II, cool regime.

which was not significantly different from one (Fig. 24), and apparently there was the same gene action as for fruit diameter in warm. The level of dominance for parents was B, I and C from low to high. The correlation coefficient was 0.83 indicating the recessive genes were operating in the direction of increased diameter of the fruit.

(b) Genetic Parameters and Estimators

Considering the growth component stages in both temperature regimes, the components of variation and their proportions, upon which the graphical treatment was based, are given in Tables 13 to 16. The proportions should reflect and in part summarize the results of the graphical analysis. The genetic parameters and estimators for the experiment in the warm regime as shown in Tables 13 and 14 can be summarized for each stage as follows:

Stage 1, warm: Examining the genetic parameters (Table 13) it is seen that $D<H_1$, which indicated overdominance; and $F<0$, which indicated the relative frequencies of recessive alleles were high. Considering the estimators (Table 14), the $H_2/4H_1$ value of 0.25, indicated that the average proportion of dominant and recessive alleles was equal in the parents; $(H_1/D)^{\frac{1}{2}}$, as an estimate of the average degree of dominance over all loci, and in this stage has a value of 1.58, which being larger than one indicated overdominance; $(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}}-F$ was 0.99, which was near enough to one, to imply that the ratio of the total number of dominant and recessive alleles in the parents was equal; the heritability was 0.2 which is relatively low; and the h^2/H_2 value was 1.4 indicating that at least one to 2

TABLE 13. Means and standard deviations for the diallel cross parameters derived from the data on days required for 7 growth stages in the warm regime of the greenhouse Experiment I.

	Parameter			
Stage	D	H_1	H_2	F
1	0.58±0.17	1.45±0.55	1.41±0.52	-0.01±0.46
2	-0.05±0.10	1.51±0.33	1.28±0.31	-0.11±0.27
3	60.69±5.88	30.03±18.69	26.89±17.63	25.65±15.67
4	4.47±2.50	13.16± 7.96	11.46± 7.51	2.68± 6.68
5	1.68±0.34	1.49± 1.07	1.38± 1.01	0.16± 0.90
6	40.78±4.20	3.66±13.35	3.41±12.59	0.89±11.19
7	0.89±0.20	0.43± 0.63	0.40± 0.60	0.33± 0.53

TABLE 14. The diallel cross estimators from the data of the warm regime of the greenhouse Experiment I, (Table 13).

	Estimator				
Stage	$(H_1/D)^{\frac{1}{2}}$	$H_2/4H_1$	$\frac{(4DH_1)^{\frac{1}{2}}+F}{(4DH_1)^{\frac{1}{2}}-F}$	heritability	h^2/H_2
1	1.58	0.25	0.99	0.21	1.4
2	5.61	0.21	0.65	-0.02	1.6
3	0.70	0.22	1.86	0.84	2.8
4	1.72	0.22	1.42	0.15	2.0
5	0.94	0.23	1.11	0.39	3.6
6	0.30	0.23	1.08	0.83	3.6
7	0.69	0.24	1.74	0.63	4.0

genes controlling this stage exhibited some degree of dominance.

Stage 2, warm: The values of parameters (Table 13) indicated the same genetic information as from Stage 1, warm. Considering the estimators, $(H_1/D)^{\frac{1}{2}}$ = 5.61 (Table 14), and being larger than one, means overdominance over all loci; $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 0.65, which was less than one, and indicated more recessive than dominant genes in the parents. There was a very low and negative heritability of -0.02 for this stage, and h^2/H_2 = 1.6 indicating at least 2 genes exhibited some degree of dominance.

Stage 3, warm: The summary of results was $D>H_1$ (Table 13), which indicated partial dominance; $F>0$ which indicated that the parents carried an excess of dominant over recessive genes; and $H_1>H_2$, meaning unequal allele frequencies. The estimators showed $H_2/4H_1$ = 0.22 (Table 14) which indicated a highly asymmetrical distribution of the dominant and recessive alleles in the parents; $(H_1/D)^{\frac{1}{2}}$ was 0.70, and being greater than zero but less than one, indicated partial dominance; $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 1.86, and being larger than one, indicated more dominant than recessive genes controlled this stage. The heritability was 0.84 indicating that highly inheritable genetic variation existed. A value of 2.8 for h^2/H_2, means that there were at least 3 genes exhibiting some degree of dominance.

Stage 4, warm: The parameters (Table 13) showed $D<H_1$, which indicated overdominance, and $F>0$ showing that the parents carried more dominant than recessive genes to affect this stage. The estimators (Table 14) show $H_2/4H_1$ = 0.22, and this low value indicated a highly asymmetrical distribution of the dominant and recessive alleles in the parents; also H_2 was smaller than H_1, hence there were unequal

allele frequencies. $(H_1/D)^{\frac{1}{2}}$ was 1.72 which is larger than one, therefore overdominance was present; and $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 1.42, which being larger than one, indicated an excess of dominant over recessive genes. The heritability for this stage was very low, only 0.15; and the h^2/H_2 value of 2.0 means that there were at least 2 genes showing some degree of dominance.

Stage 5, warm: The parameters in Table 13 showed $D>H_1$ slightly, which indicated partial to complete dominance, and $F>0$ which indicated that the parents carried more dominant than recessive genes controlling this stage; and $H_1>H_2$, meaning unequal allele frequencies. The estimators show $H_2/4H_1 = 0.23$ (Table 14) which indicated a highly asymmetrical distribution of the dominant and recessive alleles in the parents. $(H_1/D)^{\frac{1}{2}}$ was 0.94, and being smaller than but very close to one, indicated that the estimate of the average degree of dominance over all loci was partial but almost complete. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 1.11, and being a little larger than one, indicated a slightly greater number of dominant over recessive genes affected Stage 5. The heritability for this stage was 0.39, and a value of 3.6 for h^2/H_2 means that there were at least 4 genes showing some degree of dominance.

Stage 6, warm: The parameters from this stage had the same trends as those for Stage 3, warm, therefore must have the same gene action. The estimators show $H_2/4H_1 = 0.23$ (Table 14), which indicated an asymmetrical distribution; $(H_1/D)^{\frac{1}{2}}$ was 0.30 and being larger than zero but smaller than one, indicated partial dominance. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 1.08, slightly larger than one indicating a slightly greater number of dominant than recessive genes. The heritability for this

stage was very high, being 0.83; and the h^2/H_2 was 3.6 indicating that at least 4 genes were exhibiting some degree of dominance.

Stage 7, warm: The characteristics of the parameters for this stage were similar to those for Stage 6, warm. The estimators show $H_2/4H_1$= 0.24 (Table 14), which indicated a highly asymmetrical distribution of the dominant and recessive alleles in the parents. $(H_1/D)^{\frac{1}{2}} = 0.69$ which indicated partial dominance; and $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 1.74 which being larger than one, indicated more dominant than recessive genes. The heritability was 0.63 and h^2/H_2 was 4.0 indicating that at least 4 genes showed some degree of dominance.

Stage 1, cool: The parameters (Table 15) showed $D \leq H_1$, which indicated overdominance; and F=1.75, which being larger than zero indicated the parents carried more dominant than recessive genes which affected growth in this stage. $H_1 > H_2$, hence there were unequal allele frequencies. $H_2/4H_1 = 0.22$ (Table 16) and this low value indicated an asymmetrical distribution of the dominant and recessive alleles in the parents. $(H_1/D)^{\frac{1}{2}} = 1.70$, which is larger than one and indicated overdominance. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F = 1.84$, which indicated more dominant than recessive genes affected this growth stage. The heritability was 0.25 and the h^2/H_2 was 2.8 indicating that at least 3 genes were exhibiting some degree of dominance.

Stage 2, cool: It is seen that $D > H_1$ (Table 15), which indicated partial dominance; F=-0.95, and being less than zero indicated that relative frequencies of recessive alleles were higher than those for dominant alleles. $H_1 > H_2$, thus the positive and negative alleles for the loci controlling this stage were not in equal proportions. $H_2/4H_1 = 0.22$ (Table 16), and such a low value indicated a highly

TABLE 15. Means and standard deviations for the diallel cross parameters derived from the data on days required for 7 growth stages in the cool regime of the greenhouse Experiment I.

Stage	Parameter			
	D	H_1	H_2	F
1	1.74± 0.46	5.05± 1.48	4.54± 1.39	1.75± 1.24
2	2.34± 0.26	1.22± 0.83	1.07± 0.78	-0.95± 0.70
3	68.28± 5.79	25.30±18.43	25.01±1738	-0.87± 1.55
4	92.53± 7.10	93.77±22.58	85.98±21.30	52.25±18.94
5	5.38± 0.58	10.30± 1.84	9.58± 1.73	3.94± 1.54
6	59.25±16.77	282.7 ±53.31	226.1 ±50.30	34.87±44.71
7	1.23± 0.43	5.72± 1.36	4.70± 1.28	2.26± 1.14

TABLE 16. The diallel cross estimators from the data of the cool regime of the greenhouse Experiment I., (Table 15).

Stage	Estimator				
	$(H_1/D)^{\frac{1}{2}}$	$H_2/4H_1$	$\frac{(4DH_1)^{\frac{1}{2}}+F}{(4DH_1)^{\frac{1}{2}}-F}$	heritability	h^2/H_2
1	1.70	0.22	1.84	0.25	2.8
2	0.72	0.22	0.56	0.37	2.4
3	0.61	0.25	0.98	0.64	5.6
4	1.01	0.22	1.78	0.65	3.6
5	1.38	0.23	1.72	0.42	3.6
6	2.18	0.20	1.31	0.19	0.8
7	2.15	0.21	2.47	0.20	0.8

asymmetrical distribution of the dominant and recessive alleles in the parents. $(H_1/D)^{\frac{1}{2}}$ = 0.72, being smaller than one, indicated partial dominance; $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ = 0.56 and being smaller than one, implied more recessive than dominant genes were involved. The heritability was 0.37 and h^2/H_2 was 2.4 which indicated at least 2 to 3 genes were exhibiting some degree of dominance.

Stage 3, cool: The parameters for this stage (Table 15) showed the same trends as those for Stage 2, cool, and therefore both stages must have had the same gene action. $H_2/4H_1$ = 0.25 (Table 16) and indicated that the average proportion of dominant and recessive allels was equal in the parents. $(H_1/D)^{\frac{1}{2}}$ was 0.61 and, being less than one but more than zero, suggested partial dominance in action over all loci. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ = 0.98, which was near enough to one to imply that there was an equal number of recessive and dominant genes involved. The heritability was 0.64, and there were at least 6 genes exhibiting some degree of dominance.

Stage 4, cool: The parameters for this stage (Table 15) showed the same characteristics as those for Stage 1, cool, therefore both stages must have had the same gene action. The estimators (Table 16) showed $H_1/4H_2$ = 0.22, a relatively low value, which indicated a highly asymmetrical distribution of dominant and recessive alleles in the parents. $(H_1/D)^{\frac{1}{2}}$ was 1.01, almost equal to one, thus indicating that complete dominance was present. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ = 1.78, and being greater than one, indicated a greater number of dominant than recessive genes were involved. The heritability was 0.65, and the h^2/H_2 was 3.6 implying that at least 4 genes showed some degree of dominance.

Stage 5, cool: The characteristics of the parameters for Stage 5, cool (Table 15) were similar to those for Stage 4, cool, indicating similar gene action in both stages. The estimators (Table 16) showed $H_2/4H_1 = 0.23$, meaning a highly asymmetrical distribution of the dominant and recessive alleles in the parents; $(H_1/D)^{\frac{1}{2}}$ was 1.38, and being larger than one, implied overdominance; and $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 1.72, which indicated that more dominant than recessive genes were affecting this stage. The heritability was 0.42, and the h^2/H_2 was 3.6 implying that at least 4 genes showed some degree of dominance.

Stage 6, cool: Again the characteristics of the parameters for Stage 6, (Table 15) cool, were similar to those Stage 4, cool, thus gene action must have been similar in Stages 4, 5 and 6, in cool. Values in Table 16 showed $H_2/4H_1 = 0.20$ and indicated unequal distribution of the dominant and recessive alleles in the parents; $(H_1/D)^{\frac{1}{2}} = 2.18$ which being larger than one, implied overdominance was present; and $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 1.31, and being larger than one, indicated more dominant than recessive genes affecting earliness of this stage. The heritability for this stage was 0.19 and the h^2/H_2 was 0.8 implying that at least one gene was exhibiting some degree of dominance.

Stage 7, cool: It is seen (Table 15) that $D<H_1$, which indicated overdominance; F=2.26, and being larger than one, indicated the parents carried more dominant than recessive genes affecting this stage. $H_1>H_2$ and also $H_2/4H_1 = 0.21$ (Table 16) which indicated an asymmetrical distribution of the dominant and recessive alleles in the parents; $(H_1/D)^{\frac{1}{2}} = 2.15$, and being larger than one, indicated overdominance; and $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 2.47 which being larger than one,

indicated a greater number of dominant than recessive genes involved. Heritability was 0.20 for this stage, and the value of h^2/H_2 was 0.8 which indicated at least one gene exhibited some degree of dominance.

(B) Greenhouse Experiment II

Greenhouse Experiment II was concerned with the days required for plants to progress through growth Stages 5 and 6 in two temperature regimes, and using artificial pollination throughout the experiment.

Stage 5, warm: The parameters for this stage (Table 17) showed the same trends as those for greenhouse Experiment I, therefore both stages must have had the same gene action. $H_2/4H_1 = 0.19$ and indicated an asymmetrical distribution of the dominant and recessive alleles in the parents; $(H_1/D)^{\frac{1}{2}} = 0.98$, very close to one, indicated almost complete dominance. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was 1.72 and being larger than one indicated more dominant than recessive genes affected earliness. The heritability was 0.39, and at least one of the genes involved in the earliness exhibited some degree of dominance.

Stage 6, warm: Again the same gene action as in Stage 6, warm, in the greenhouse Experiment I is shown by the characteristics of the parameters (Table 17). $H_2/4H_1 = 0.24$, and this very low value indicates an asymmetrical distribution; $(H_1/D)^{\frac{1}{2}} = 0.18$ and being larger than zero implied partial dominance $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F = 1.72$, and being larger than one, indicated more dominant than recessive genes were involved. The heritability was the high value of 0.77, and the h^2/H_2 was 4.80 which indicated at least 5 genes exhibited some degree of dominance.

TABLE 17. Means and standard deviations for the diallel cross parameters and estimators from warm and cool regimes in greenhouse Experiment II.

Stage	Parameter/Estimator	Temperature	
		warm	cool
	D	1.06 ± 0.18	1.85 ± 0.44
	H_1	1.02 ± 0.58	1.47 ± 1.39
	H_2	0.79 ± 0.55	1.20 ± 1.31
	F	0.55 ± 0.49	-0.10 ± 1.17
5	$(H_1/D)^{\frac{1}{2}}$	0.98	1.04
	$H_2/4H_1$	0.19	0.20
	$(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$	1.72	0.93
	heritability	0.39	0.27
	h^2/H_2	0.80	0.40
	D	40.16±11.46	9.03± 5.12
	H_1	-1.29± 3.64	34.78±16.27
	H_2	-1.35±33.43	28.14±15.35
	F	3.81± 3.05	-14.78±13.64
6	$(H_1/D)^{\frac{1}{2}}$	0.18	1.96
	$H_2/4H_1$	0.24	0.20
	$(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$	1.72	0.41
	heritability	0.77	0.12
	h^2/H_2	4.80	0.40

Stage 5, cool: The parameters for this stage show the same trends as those for Stage 5 in greenhouse Experiment I; thus the same gene action must have been present. $(H_1/D)^{\frac{1}{2}} = 1.04$ (Table 17), and being larger than one, indicated overdominance; and $H_2/4H_1 = 0.20$, and this low value indicated an asymmetrical distribution of the dominant and recessive alleles in the parents. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F = 0.93$, which implied almost equal numbers of dominant and recessive alleles among parents, and the recessive genes had a little higher frequency than the dominant. The heritability was 0.27 and at least one gene showed some degree of dominance.

Stage 6, cool: The parameters for this stage (Table 17) show the same trends as the greenhouse Experiment I Stage 6, thus the same gene action was present. $(H_1/D)^{\frac{1}{2}} = 1.96$, which indicated overdominance; $H_2/4H_1 = 0.20$ and this low value indicated a highly asymmetrical distribution of the dominant and recessive alleles. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F = 0.41$, and being smaller than one, indicated more recessive than dominant genes affecting earliness. The heritability was 0.12, and at least one gene showed some degree of dominance.

Days Required per Plastochron in Both Temperature Regimes

In the warm regime the parameters (Table 18) show D was almost equal to H_1 indicating complete dominance; $H_1<H_2$, therefore there were not equal proportions of positive and negative alleles in the parents, and $F<0$, meaning that the relative frequencies of recessive alleles were high. $(H_1/D)^{\frac{1}{2}}$ is 0.92 which is very near to one and means almost complete dominance was present. $H_2/4H_1 = 0.19$, and this low value indicated an asymmetrical distribution of the

TABLE 18. Means and standard deviations for the diallel cross parameters and estimators from warm and cool regimes for days required per plastochron.

Parameter and Estimator	Temperature	
	warm	cool
D	-0.15±0.08	0.01±0.02
H_1	-0.13±0.24	0.16±0.06
H_2	-0.10±0.23	0.16±0.06
F	-0.20±0.20	0.03±0.05
$(H_1/D)^{\frac{1}{2}}$	0.92	4.90
$H_2/4H_1$	0.19	0.26
$(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$	0.15	0.38
heritability	-0.16	0.02
h^2/H_2	2.0	5.6

TABLE 19: Means and standard deviations for the diallel cross parameters and estimators from warm and cool regimes for fruit weight and fruit diameter.

Parameters and Estimators	Temperature			
	warm		cool	
	fruit weight	fruit diameter	fruit weight	fruit diameter
D	1423.9±246.4	130.4±21.0	7992.5±4492.1	315.2±19.0
H_1	334.1±783.6	7.9± 6.7	3583.6±1564.9	84.0±60.4
H_2	264.5±739.3	4.7± 6.3	3196.5±1476.4	73.0±57.0
F	-459.3±657.1	-40.1±55.9	3150.9±1312.3	102.7±50.7
$(H_1/D)^{\frac{1}{2}}$	0.48	0.25	0.67	0.52
$H_2/4H_1$	0.20	0.15	0.22	0.22
$(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$	0.50	0.23	1.83	1.92
heritability	0.44	0.48	0.91	0.97
h^2/H_2	0.4	8.8	2.8	2.0

dominant and recessive alleles. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F = 0.15$, and since this value was less than one, there must have been more recessive than dominant genes involved. The heritability was -0.16 and at least 2 genes showed some degree of dominance.

In the cool regime $D<H_1$ (Table 18), indicating overdominance; H_1 was equal to H_2, meaning that positive and negative genes were present in equal numbers; and $F<0$, which indicated relative frequencies of recessive alleles were high. $(H_1/D)^{\frac{1}{2}} = 4.9$, and being greater than one, indicated overdominance; and $H_2/4H_1 = 0.19$, a very low value associated with a highly asymmetrical distribution of the dominant and recessive alleles in the parents. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F = 0.38$, and being less than one, indicated a greater number of recessive than dominant genes were involved. The heritability for this stage was very low, only 0.02, and at least 6 genes exhibited some degree of dominance.

Fruit Weight and Diameter in Both Temperature Regimes

In the warm regime, the values in Table 19 show that $D>H_1$, which indicated partial dominance; $H_1>H_2$, which indicated unequal numbers of dominant and recessive genes were involved; and $F<0$, which meant that relative frequencies of recessive alleles were high; $(H_1/D)^{\frac{1}{2}} = 0.48$ and 0.25, and both being larger than zero but smaller than one indicated partial dominance; $H_2/4H_1$ for both characteristics was very low, 0.20 and 0.15, and indicated asymmetrical distribution of dominant and recessive genes; and $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F = 0.50$ and 0.23, which were smaller values than one, therefore there must have had more recessive than dominant genes affecting each of the characteristics.

Heritability for fruit weight was 0.44 and for fruit diameter was 0.48, and at least one gene and nine genes were exhibiting some degree of dominance affecting fruit weight and diameter respectively.

In the cool regime, the values in Table 19 show that $D>H_1$, which suggested partial dominance; $H_1>H_2$, thus unequal numbers of positive and negative alleles were involved; and $F>0$, which indicated that the parents carried more dominant than recessive genes which influenced the characteristics. The estimators $(H_1/D)^{\frac{1}{2}} = 0.67$ and 0.52 for fruit weight and diameter respectively, and both values were between zero and one which indicated partial dominance; and $H_2/4H_1$ for both characters was 0.22, a very low value which indicated asymmetrical distribution of the dominant and recessive alleles in the parents. $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F = 1.83$ and 1.82, and both values being larger than one, indicated more dominant genes than recessive genes influenced fruit weight and diameter. The heritability values for these two characteristics were 0.91 and 0.97, and h^2/H_2 values indicated at least 3 and 2 genes were exhibiting some degree of dominance in fruit weight and diameter respectively.

B. Griffing's Method

The results from the application of Griffing's method showed a large number of significant effects for general combining ability (G.C.A.) and specific combining ability (S.C.A.) which emphasize hereditary differences in the individual stages of different genotypes or cultivars. G.C.A. and S.C.A. for each of the 7 growth component stages in the warm regime were all significant (Table 20). Also the differences between reciprocal crosses were only significant

TABLE 20. Mean squares for general (G.C.A.) and specific (S.C.A.) combining ability for the growth component stages in warm and cool regimes.

Stage	G.C.A.		S.C.A.		Reciprocal Effects	
	Temperature					
Stage	warm	cool	warm	cool	warm	cool
1	3.3*	3.6*	3.1*	8.9*	0.2	1.6
2	1.8*	88.3*	2.7*	38.7*	5.9*	68.4*
3	230.5*	419.2*	56.3*	56.1*	2.5	4.3
4	17.9*	293.0*	26.1*	172.1*	7.0	34.7*
5	7.8*	13.4*	3.2*	18.9*	0.6	1.7*
6	242.6*	489.0*	7.4*	453.5*	8.0*	4.6
7	3.6*	0.4	1.0*	11.8*	0.1	0.9*

* significant at 5% level

TABLE 21: Mean squares for general (G.C.A.) and specific (S.C.A.) combining ability for the Stages 5 and 6 after hand-pollination treatment in warm and cool regimes.

Stage	G.C.A.		S.C.A.		Reciprocal Effects	
	Temperature					
	warm	cool	warm	cool	warm	cool
5	4.7*	11.8*	1.9*	2.0	1.1*	1.4
6	217.5*	188.4*	2.1	61.8*	10.1	9.7

* significant at 5% level

in Stages 2 and 6. In the cool regime, both G.C.A. and S.C.A. in all stages showed significant effects except for Stage 7 (Table 20), and for the reciprocal crosses, Stages 2, 4, 5 and 7 showed significant differences.

Regarding days required for Stages 5 and 6 after the hand pollination treatment (Table 21), there were significant effects for the G.C.A. In both regimes; however the S.C.A. was less variable and only Stage 5, warm, and Stage 6, cool, showed significant effects. The reciprocal effects were not significant except for Stage 5, warm.

Considering days required per plastochron, the G.C.A., S.C.A. and reciprocal effects were significant (Table 22) in the warm regime, whereas in the cool regime, only the S.C.A. and reciprocal effects were significant.

Considering fruit weight and diameter, the G.C.A. showed significant effects under both temperature regimes (Table 23), however the S.C.A. showed significant effects on the two characteristics in the cool regime only. No differences were significant between the reciprocals for fruit weight and diameter in either temperature regime.

C. Net Photosynthesis Rate in Warm and Cool Regime Growth Chambers

Space limitation precluded replication, thus the data in this experiment were not analyzed statistically. Inspection of the data from the warm regime (Table 24) shows that the net photosynthesis rate fluctuated with the different plastochrons, and had a peak and a lowest point every 2 to 4 plastochrons. For example, B had an increased photosynthesis rate starting from the 4th plastochron to

TABLE 22. Mean squares for general (G.C.A.) and specific (S.C.A.) combining ability effects for days required per plastochron in warm and cool regimes.

Source of variance	Temperature	
	warm	cool
G.C.A.	0.3*	0.2
S.C.A.	0.3*	0.4*
Reciprocal Effects	0.1*	0.4*

* significant at 5% level

TABLE 23: Mean squares for general (G.C.A.) and specific (S.C.A.) combining ability effects for fruit weight and diameter in warm and cool regimes.

Source of Variance	Temperature			
	warm		cool	
	Trait			
	fruit weight	fruit diameter	fruit weight	fruit diameter
G.C.A.	11756.8*	1058.1*	31336.1*	1329.4*
S.C.A.	686.8	26.5	6508.2*	154.5*
Reciprocal Effects	254.4	8.5	109.8	9.9

* significant at 5% level

to the 6th and then dropped down at the 7th and then rose again. The I cultivar, had the lowest point at the 6th plastochron and then increased its rate. These fluctuations may be related to floral differentiation. The hybrids BI and IB showed heterosis in some stages and the fluctuation patterns were very close to those of I. The net photosynthesis rate for cultivar C was somewhat different from those of I and B, and had a peak every other plastochron, which again may be related to floral differentiation, because in accordance with the growth pattern of cultivar C, the flower clusters appeared very closely, one after another, and there was only one leaf between each of the first 3 to 4 clusters.

The leaf area data from this diallel cross experiment (Table 24) show some trends. Taking the 8th plastochron for an example, cultivar B had the largest leaf area and I had the smallest, and all the hybrids were intermediatee between their parents except in the case of CB. There was an increase in leaf area for all the lines associated with the increase in plastochron number. In most cases, there was a slow increase followed by a marked increase in leaf area.

In the cool regime growth chamber, the net photosynthesis rate (Table 25) for all the lines was lower than in the warm regime. The hybrids showed heterosis in some plastochron ages and the fluctuation of the net photosynthesis rate varied with the hybrid line. The leaf area, as in the case of the 8th plastochron for example, was greatest for cultivar B and the smallest for I. All the hybrids were imtermediate in leaf area between their parents, with the

TABLE 24. Net photosynthesis rate and leaf area in growth chamber Experiment I in warm regime.

Lines	Trait	Plastochron 4	5	6	7	8
B	ps. rate†	10.5	12.2	12.8	9.8	10.9
	leaf area$^{\Psi}$	72	109	148	202	322
I	ps. rate†	11.1	10.0	5.5	11.1	12.0
	leaf area$^{\Psi}$	44	76	147	159	242
BI	ps. rate	12.9	9.5	7.5	7.8	8.1
	leaf area	47	88	135	233	300
IB	ps. rate	13.6	13.0	9.8	10.3	9.4
	leaf area	47	111	158	220	279
C	ps. rate	9.3	10.0	8.0	9.4	8.4
	leaf area	51	93	168	254	301
BC	ps. rate	8.2	9.0	9.6	11.7	9.0
	leaf area	46	78	109	202	305
CB	ps. rate	9.6	10.3	9.7	9.1	8.0
	leaf area	41	84	112	189	265
IC	ps. rate	7.1	6.3	6.0	8.4	8.9
	leaf area	57	82	147	175	258
CI	ps. rate	8.3	8.7	5.7	9.5	7.5
	leaf area	42	96	140	186	260

† ps. rate - net photosynthesis rate - mg CO_2/hr/dm^2

Ψ leaf area - cm^2

TABLE 25: Net photosynthesis rate and leaf area in growth chamber Experiment I in cool regime.

Lines	Trait	Plastochron 4	5	6	7	8
B	ps. rate†	6.9	6.9	7.4	4.2	5.1
	leaf areaΨ	48	96	165	298	441
I	ps. rate	5.9	6.8	3.7	3.2	3.9
	leaf area	48	70	134	179	257
BI	ps. rate	6.7	8.6	4.9	4.2	4.4
	leaf area	66	102	183	217	414
IB	ps. rate	6.7	7.1	4.7	4.6	4.1
	leaf area	65	100	170	247	325
C	ps. rate	6.4	7.3	4.2	5.3	4.8
	leaf area	49	102	150	237	332
BC	ps. rate	7.5	6.7	6.3	5.0	4.6
	leaf area	68	123	165	207	318
CB	ps. rate	7.5	6.2	5.1	5.4	4.8
	leaf area	66	81	161	282	382
IC	ps. rate	3.5	4.3	4.6	3.3	3.1
	leaf area	72	124	184	279	357
CI	ps. rate	4.9	4.4	3.8	3.8	5.5
	leaf area	64	107	142	238	296

† ps. rate - net photosynthesis rate - mg CO_2/hr/dm^2

Ψ leaf area - cm^2

exception of BC which was smaller and IC which was larger than both parents. Also at the 8th plastochron the leaf areas between reciprocals showed very large differences.

Reciprocal Crosses Experiments

1. Growth Component Stages

A. Warm Regime

The data for the reciprocal cross experiment (Table 26, and Appendix Tables 14 and 15) showed the following important differences under the warm regime. The inter-parental comparisons between B and I showed significant differences for all component stages except for Stage 5. The means show that for the 2 parental cultivars, there were large differences because I was consistently earlier than B even for Stage 5 where the difference was not significant. The intra-reciprocal comparisons between the reciprocals BI and IB, which had the same nuclear composition, but a difference in cytoplasm, showed no significant difference in earliness for any of the 7 stages (Table 26). In other words, the cytoplasms P_1 (from cultivar B) and P_2 (from cultivar I) had the same effects on the days required per stage. Differences between the maternal parents and their offspring could be attributed to differences in nuclear gene composition because both generations have the same cytoplasmic composition. In the case of I vs. IB, only Stage 3 showed a significant difference, and for B vs. BI, Stages 1, 2, 3, 4 and 7 showed significant differences for earliness. In other words, the differences between

TABLE 26. The non-orthognal comparisons for the seven growth component stages in the reciprocal cross Experiment I under warm and cool regimes.

Stage	Lines	Mean	Sums of squares			
			B vs I	BI vs IB	I vs IB	B vs BI
1	B	8.1 (20.1)†				
	I	7.2 (17.0)	4.1*	0.1	0.1	4.1*
	BI	7.2 (17.1)	(48.1*)	(5.0*)	(6.1*)	(45.0*)
	IB	7.2 (17.8)				
2	B	7.9 (9.7)				
	I	6.4 (9.2)	11.3*	0.5	1.8	7.2*
	BI	6.7 (8.6)	(1.3)	(1.8)	(7.2*)	(6.1*)
	IB	7.0 (8.0)				
3	B	32.1 (31.2)				
	I	19.0 (19.3)	858.1*	14.5	245.0*	304.2*
	BI	24.3 (25.4)	(708.1*)	(48.1*)	(423.2*)	(168.2*)
	IB	26.0 (28.5)				
4	B	32.8 (65.0)				
	I	24.3 (49.8)	361.3*	5.0	0.8	312.1*
	BI	24.9 (50.7)	(1155.2*)	(217.8*)	(281.3*)	(1022.5*)
	IB	23.9 (57.3)				
5	B	7.2 (9.5)				
	I	6.4 (10.2)	3.2	2.5	0.1	0.2
	BI	7.0 (9.1)	(2.5)	(0.2)	(9.8)	(0.8)
	IB	6.3 (8.8)				
6	B	35.6 (59.7)				
	I	32.4 (51.7)	135.2*	28.8	0.2	45.0
	BI	32.6 (41.3)	(320.0*)	(16.2)	(369.8*)	(1692.8*)
	IB	30.2 (43.1)				
7	B	9.4 (9.8)				
	I	5.6 (9.5)	72.2*	0.2	0.5	76.1*
	BI	5.5 (9.4)	(0.2)	(4.1)	(7.2)	(0.1)
	IB	5.3 (8.5)				

* significant at 5% level

† Means and sums of squares in brackets are from data from the cool regime to contrast with the unbracketed values from the warm regime.

nuclear compositions XY and YY were not as great as the differences between XY and XX.

B. Cool Regime

The data for the reciprocal cross experiment (Table 26) showed the following important differences under the cool regime, and some contrasts with the results of the same lines grown in the warm regime. The inter-parental comparisons between B and I were significantly different for Stages 1, 3, 4 and 6 only. Cultivar B required more days to complete each stage except for Stage 5, in which the results are the reverse of the observations for the warm regime. Stage 7 showed no significant difference between B and I although I was earlier than B, following the same trend as in the warm regime. For the F_1 intra-reciprocal comparison between BI and IB, significant differences in earliness for Stages 1, 3 and 4 were observed, and such differences were not observed in the warm regime. In the case of maternal parents and offspring (I vs. IB and B vs. BI) differences were significant for Stages 1, 2, 3, 4 and 6.

2. Net Photosynthesis Rate

A. Warm Regime

The differences in net photosynthesis rate between the parents B and I (Table 27 and Appendix Tables 16 and 18) were not significant until plastochrons 6, 7 and 8 developed. The differences between the reciprocal hybrids were not significant until plastochron 5 and later, 8 were developed. Considering the maternal parents vs. offspring comparisons, I vs. IB, showed differences which were all

TABLE 27. The non-orthogonal comparisons for the net photosynthesis rate in the reciprocal cross Experiment II under warm and cool regimes. (mg $CO_2/dm^2/hr$).

P.A.†	Line	Mean	Sums of squares			
			B vs I	BI vs IB	I vs IB	B vs BI
4	B	10.6 (9.9)Ψ				
	I	12.7 (9.0)	8.8	1.3	39.4*	65.7*
	BI	16.4 (10.3)	(1.4)	(1.3)	(8.6*)	(0.4)
	IB	17.2 (11.1)				
5	B	15.9 (8.7)				
	I	14.7 (9.2)	3.0	12.6*	6.7	7.2
	BI	14.0 (9.7)	(0.4)	(28.5*)	(36.9*)	(1.9)
	IB	16.5 (13.5)				
6	B	10.9 (5.7)				
	I	6.1 (11.9)	45.7*	6.2	51.7*	4.3
	BI	9.4 (10.9)	(76.9*)	(0.4)	(0.6)	(53.8*)
	IB	11.2 (11.3)				
7	B	10.6 (10.5)				
	I	20.5 (5.4)	193.7*	20.6	191.7*	19.9
	BI	7.5 (8.2)	(51.8*)	(0.8)	(9.5)	(10.3)
	IB	10.7 (7.5)				
8	B	8.3 (5.4)				
	I	9.4 (7.9)	2.6*	8.2*	1.8*	6.8*
	BI	6.5 (3.4)	(12.4*)	(4.4)	(18.9*)	(8.6*)
	IB	8.4 (14.8)				

† P.A. = plastochron age

Ψ see Table 26 notation

* significant at 5% level

significant except in plastochron 5; however, in the case of B vs. BI, only plastochrons 4 and 8 showed significant differences. The fluctuation patterns for the net photosynthesis rate in the reciprocal hybrids are shown in Fig. 25. Both hybrids showed heterosis in plastochron 4 and then a decrease until the 8th plastochron, at which stage the hybrid IB was intermediate between the parents, but BI was lower than either parent. Cultivar I had its lowest point at plastochron 6 and a peak at plastochron 7 whereas the other lines did not show such marked fluctuation.

B. Cool Regime

The differences in net photosynthesis rate between B and I (Table 27) were significant at plastochrons 6, 7 and 8 as was the case in the warm regime, but the differences between the reciprocals were significant only at plastochron 5. The I vs. IB comparison showed significant differences in plastochrons 4, 5 and 8. In the case of B vs. BI only the 6th and 8th plastochrons showed significant differences. In Fig. 26, it can be seen that the reciprocal hybrids showed heterosis for net photosynthesis rate at plastochrons 4 and 5. Then the rate was intermediate between parents in plastochrons 6 and 7, and finally lower than both parents at the 8th plastochron. Cultivar I had the lowest net photosynthesis rate at the 4th plastochron, attained a peak at the 6th, then decreased markedly at the 7th and finally increased sharply again. Cultivar B had a peak at the 7th plastochron and then decreased.

3.

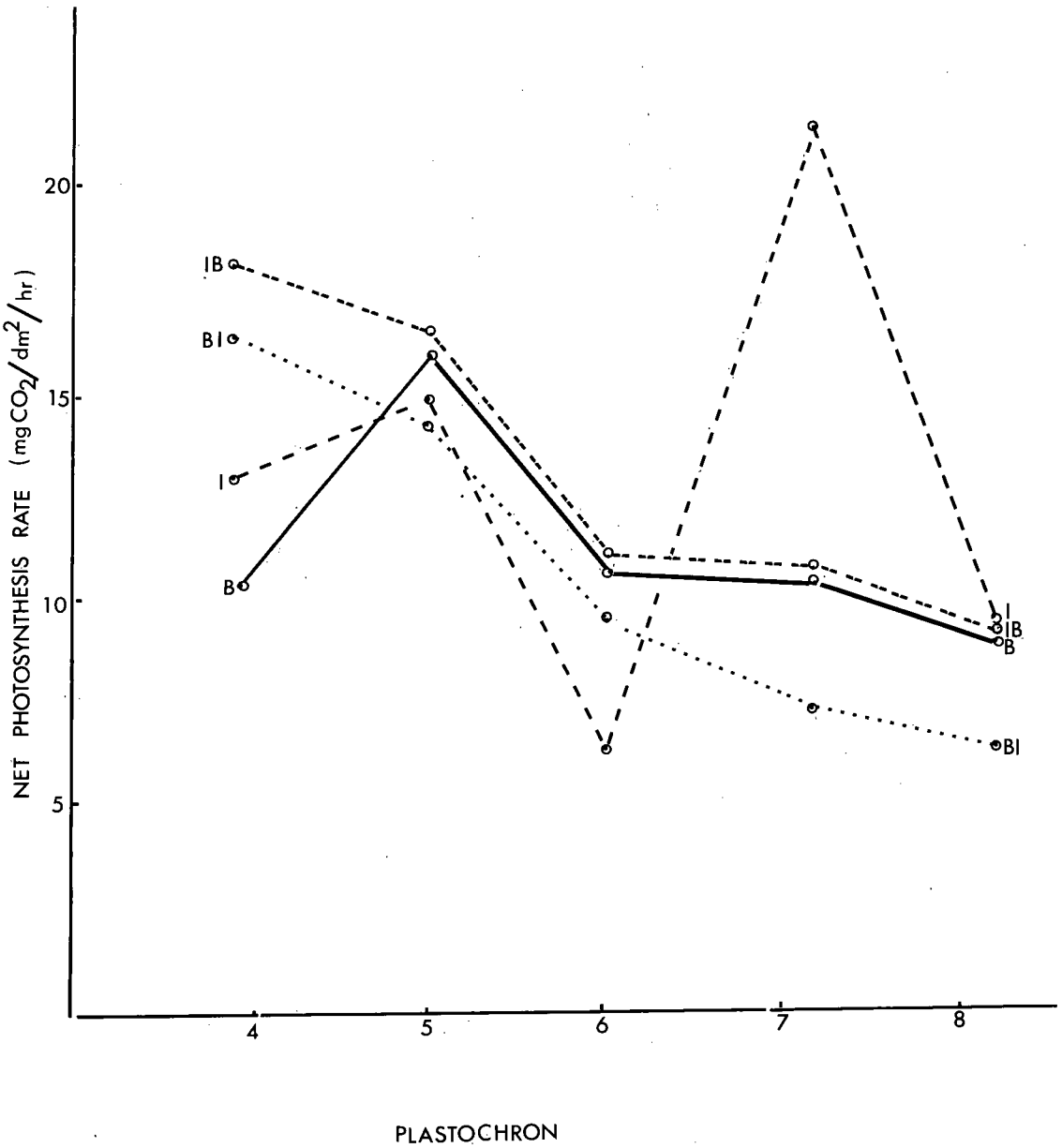

Fig. 25. Net photosynthesis rate for each plastochron of 4 lines in the warm regime.

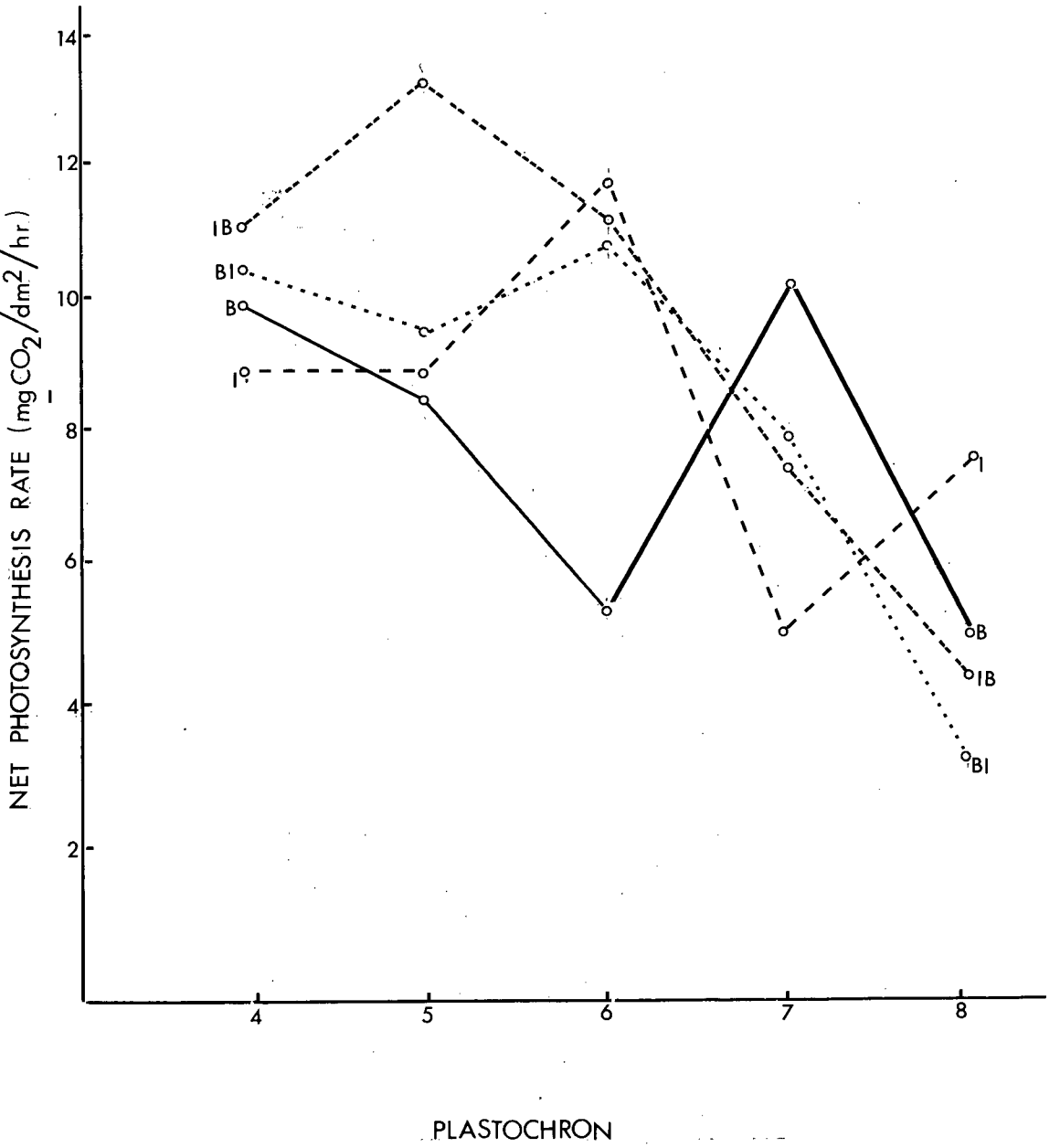

Fig. 26. Net photosynthesis rate for each plastochron of 4 lines in the cool regime.

3. Leaf Area

A. Warm Regime

The leaf area differences between parents B and I were significant for plastochrons 5 to 8 (Table 28 and Appendix Tables 17 and 19). There were no significant differences between the reciprocals in any of the plastochrons. Comparing maternal parents and their offspring, I vs. IB, showed significant differences for all plastochrons except in the 4th, and in the case of B vs. BI, only the 4th and 8th plastochrons showed significant differences in leaf areas. In Fig. 27, at plastochron 4, cultivar B had the largest leaf area, and the reciprocal hybrids had smaller leaf areas than both parents. Leaf area in all the lines increased sharply from the 5th plastochron, except I which increased sharply at the 6th. Thy hybrid, BI, showed heterosis for leaf area at the 7th and 8th plastochrons.

B. Cool Regime

The leaf area differences between parents B and I (Table 28) were significant for all plastochrons. There were significant differences between the reciprocal hybrids at the 7th and 8th plastochrons only. Comparing the differences in leaf area between maternal parents and their offspring, I vs. IB, had significant differences at all plastochrons except at the 5th, but in the case of B vs. BI, only the differences at the 5th and 8th plastochrons were significant. In Fig. 28, it is obvious that both hybrids showed heterosis when their leaf areas increased sharply at plastochrons 7 and 8. Cultivar I had the smaller leaf areas from the 4th to the 8th plastochron.

TABLE 28: The non-orthogonal comparisons for the leaf area in the reciprocal cross Experiment II under warm and cool regimes. (cm^2).

P.A.†	Line	Mean	Sums of squares			
			B vs I	BI vs IB	I vs IB	B vs BI
4	B	62.2 (57.5)Ψ				
	I	50.5 (36.8)	276.1	36.1	112.5	450.1*
	BI	47.2 (60.0)	(861.1*)	(128.0)	(1081.1*)	(60.5)
	IB	43.0 (52.0)				
5	B	95.2 (114.3)				
	I	65.7 (88.5)	1770.1*	0.5	1512.5*	6.1
	BI	93.8 (98.5)	(1526.1*)	(98.0)	(200.0)	(1035.1*)
	IB	93.2 (91.5)				
6	B	154.0 (166.5)				
	I	97.0 (115.8)	6498.0*	112.5	5050.1*	406.1
	BI	139.7 (156.0)	(5151.1*)	(1.1)	(3240.1*)	(253.1)
	IB	147.2 (155.3)				
7	B	242.5 (186.8)				
	I	164.5 (165.3)	12324.5*	288.0	11552.0*	180.5
	BI	252.0 (224.3)	(924.5*)	(1431.1*)	(6962.0*)	(231.1)
	IB	240.0 (197.5)				
8	B	373.0 (213.8)				
	I	284.0 (191.3)	15931.1*	288.0	23220.0*	1810.5*
	BI	403.1 (274.0)	(1012.5*)	(2043.0*)	(13695.0*)	(1596.1*)
	IB	391.7 (242.0)				

† P.A. = plastochron age

Ψ see Table 26 notation

* significant at 5% level

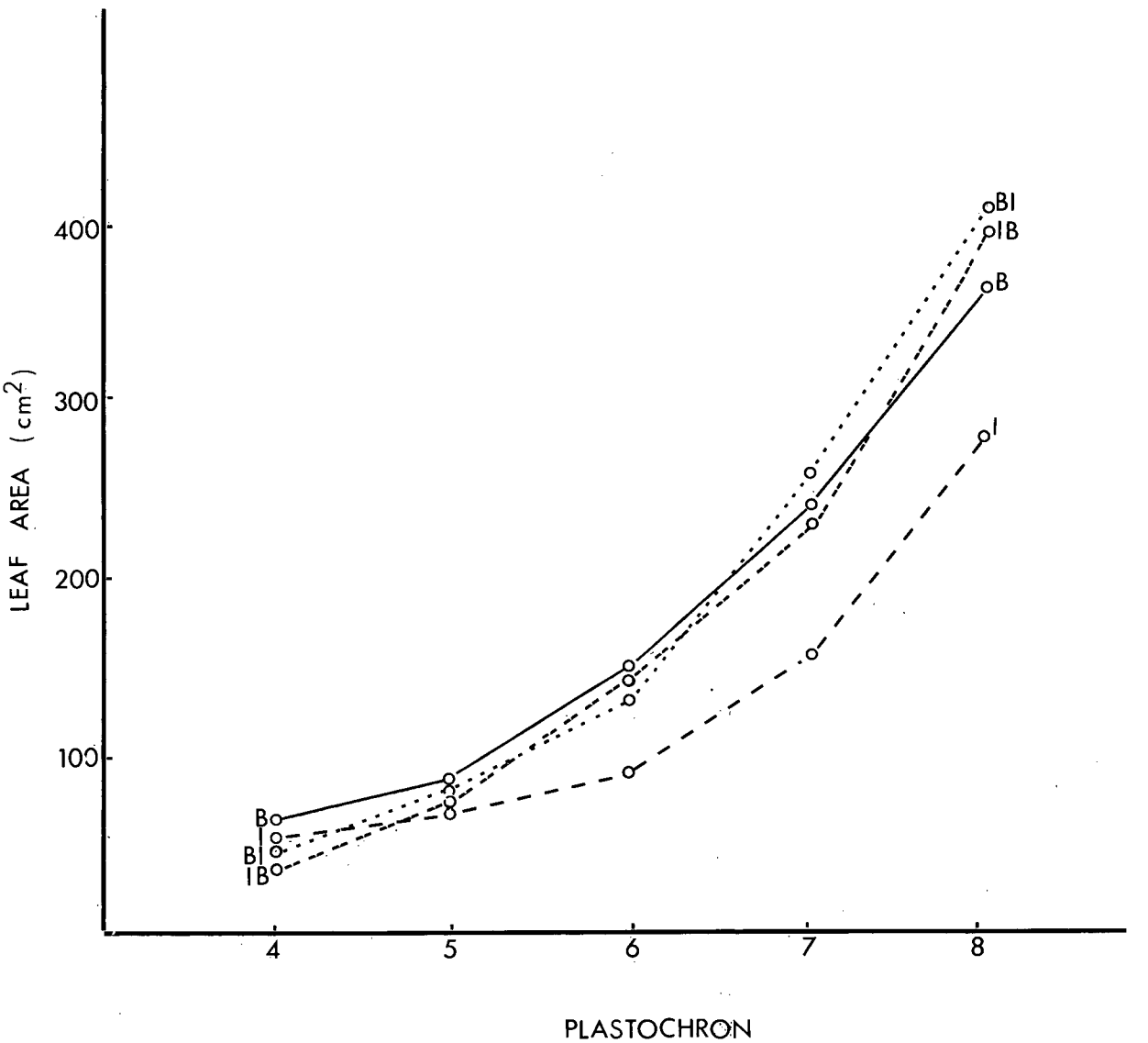

Fig. 27. Leaf area at each plastochron among the lines in warm regime.

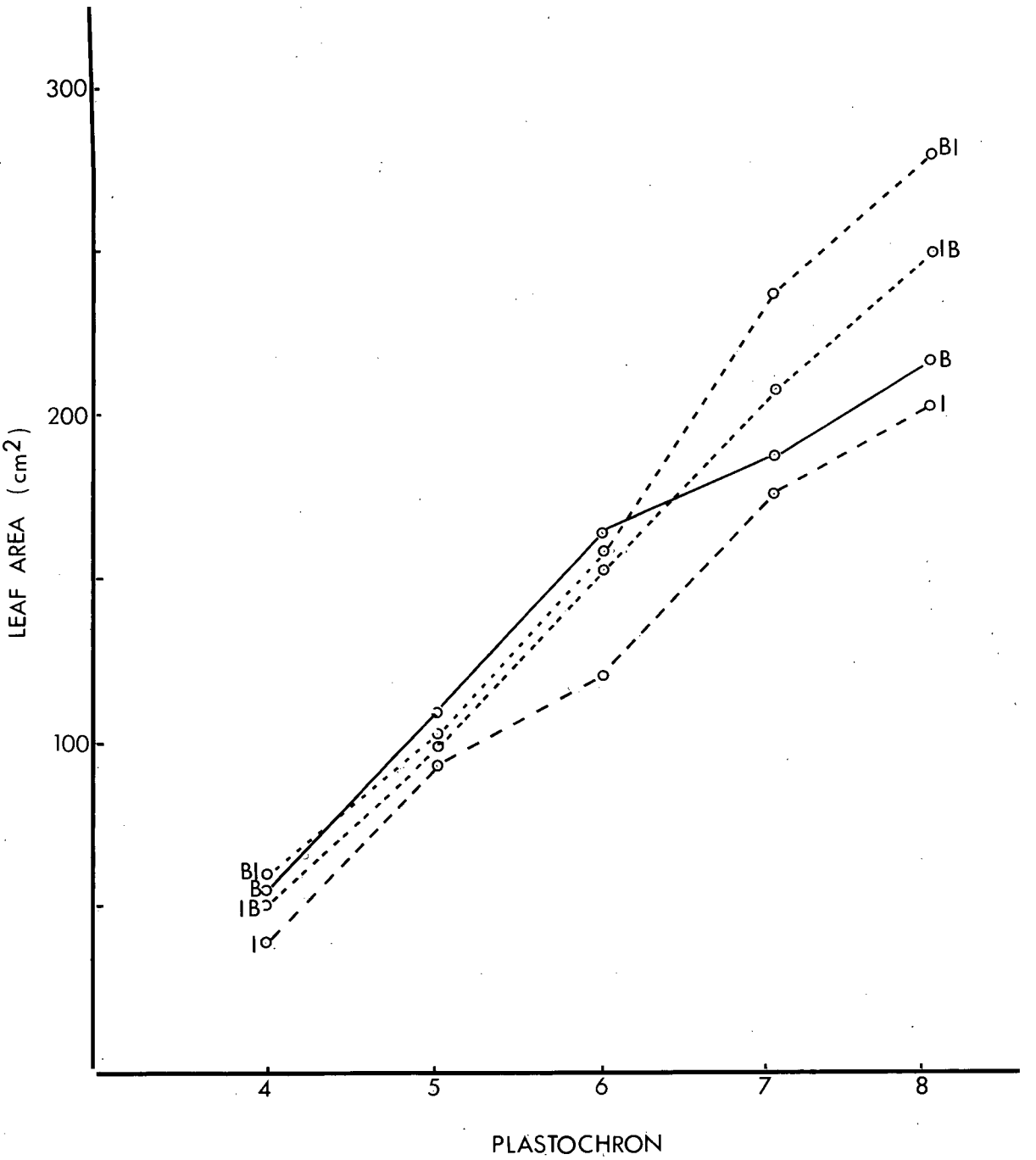

Fig. 28. Leaf area of each plastochron among the lines in cool ~~regime~~ temperature regime.

Field Experiments

1. Experiment I

Field Experiment I was handled in two parts. Part 1 examined 8 lines which included parents, B and I; their reciprocal hybrids IB and BI, and the backcrosses IBxI, BIxI, BIxB and IBxB. The days required for the Stages A and C were recorded for all 12 plants in each line and the data are shown in Table 23 of the Appendix. The comparison among the line means (Table 29) showed large differences in the days required for both stages for the 2 parents, I and B, and I was earlier than B. The differences between reciprocal hybrids were very small and both of the hybrids were intermediate between their parents. Both the reciprocal hybrids were earlier if backcrossed to the early parent, I, than if backcrossed to the late parent B. One of the backcross progenies IBxI was very close to the early parent I for the two stages, whereas another progeny BIxB was

TABLE 29: Mean days required for Stages A and C in the field Experiment I, part 1.

	Line							
Stage	I	B	IB	BI	IBxI	BIxI	IBxB	BIxB
A	68.9	80.8	74.6	74.8	69.5	70.6	76.8	79.5
B	47.3	59.7	52.3	51.0	48.4	50.5	53.3	55.5

closer to the late parent B in Stages A and C.

Part 2 examined two segregating generations of the reciprocals BI and IB, denoted BIF_2, IBF_2, BIF_3 and IBF_3. The means for

the earliness in Stages A and C for each of the 4 progenies were based on 100 plants in each progeny. The mean number of days required for BIF_2 and IBF_2 in both stages (Table 30) were very similar, but these reciprocals showed larger differences in the F_3 generation, and were earlier than the F_2 generation. The F_3 standard deviations for the F_3 were larger than those for the F_2, which indicated that segregation was continuing. Since there were larger ranges for the F_3 than for the F_2 in both stages, then the selection for earliness would be more effective in the F_3. The plants which were earlier than the parents for Stages A and/or C were subjected to pedigree selection, that is seed from each individual plant selection was kept separate for the next generation. In the IBF_3 population, 6 early plants were selected, and similarly in the BIF_3, 11 early plants were selected.

TABLE 30: The mean number of days required for Stages A and C in the field Experiment I, part 2.

Line	Stage A	Stage C
BI F_2	75.1±4.0	49.9±4.8
IB F_2	75.6±4.8	49.1±4.6
BI F_3	72.1±8.7	49.2±5.5
IB F_3	70.7±7.7	51.1±5.1

2. Experiment II

The progenies from the 17 individual plants selected from the F_3 reciprocal populations in Experiment I, part 2 (1971), were grown in the field (1972) in plots with 25 plants per progeny.

The mean for the IB F_4 Stage A was 66.6 ± 5.7 days and for Stage C was 49.5 ± 3.4 days (Table 31). The BI F_4 Stage A was 66.8 ± 6.8 days and Stage C 47.3 ± 4.7 days. These means were all intermediate between those of the original parents B and I, but had the tendency to be closer to the early parent I. Approximately 10% of the earliest segregates of the IB F_4 and BI F_4 were pedigree selected for earliness and used to provide the F_5 progenies.

TABLE 31: Means, heritability, selection progress and genetic progress in F_4 generations.

	IB F_4		BI F_4	
	Stage A	Stage C	Stage A	Stage C
Mean	66.6±5.7	49.5±3.4	66.8±6.8	47.3±4.7
h^2	0.63	0.57	0.81	0.66
σp (days)	5.70	3.40	6.80	4.70
i	1.75	1.75	1.75	1.75
ΔG (days)	6.30	3.40	9.60	5.40
σG (days)	4.60	2.60	6.20	3.80

The heritabilities for both Stages A and C in the reciprocal cross populations were relatively high, but Stage A had higher heritabilities than Stage C (Table 31). The calculated or expected selection progress, ΔG, [following the models of Falconer (1967) and Pirchner (1969), as shown on page 447] was 6.30 days in Stage A and 3.40 days in Stage C for IB F_4 selections, and 9.60 days and 5.40 days for BI F_4 selections in Stages A and C respectively. The genetic

progress, σ_G, was 4.60 days and 2.60 days for Stages A and C respectively in the IB F_4; but was 6.20 and 3.80 days for Stages A and C in the BI F_4.

3. Experiment III

Part 1. Seed from the earliest 10% of the IB F_4 and BI F_4 which were pedigree selected in 1972 was used in this Part of the experiment. The means (Table 32) for Stages A and C in the IB F_5 were 60.3 and 50.5 days respectively, and similarly 61.0 and 49.2 days for the same stages of the BI F_5 in 1973. All these means were earlier than both of the parents, B and I, indicating that selection for the shortest length recombinations was being realized.

Part 2. Six lines from the F_4 generation selected for earliness (in 1972) were compared to two lines selected for lateness from the F_4 generation (Tables 32). The means of the six selected early lines for both stages A and C were all earlier than both parents, except one line (II-22-B) showed one day later than the earlier parent I in Stage A. The two latest lines in both stages were all intermediate between their original parents B and I, but showed the tendency of being closer to the later parent B. All the means of these selected F_5 pedigree genes for earliness were no earlier than their F_4 parents, although some of the plants within each line were close to the parent value. These differences are confounded with season, but the data may indicate a minimal number of days are required to grow through a certain stage, and selection may not able to go beyond this threshold.

TABLE 32: Mean days required for selections made for Stages A and C in the F_5 of the field Experiment III.

Part 1. Mass Populations

Stage	Parental line	Mean (days)
A	B	74.0±2.0
	I	62.0±2.2
	BI F_5	61.0±3.5
	IB F_5	60.3±3.3
C	B	61.0±4.4
	I	52.6±3.7
	BI F_5	49.2±3.7
	IB F_5	50.5±4.4

Part 2. Pedigree Populations

Stage	Parental line	Line No.†	Mean (days)
A	B		74.0±2.0
	I		62.0±2.2
	IB F_5	I-48-18	59.6±3.3
	BI F_5	II-53-20	60.6±3.2
	BI F_5	II-53-19	60.8±1.9
	BI F_5	II-53-22	61.8±3.2
	BI F_5	II-22-1	58.3±2.8
	BI F_5	II-22-13	63.2±4.0
	IB F_5	I-26-16	71.2±1.9
	BI F_5	II-50-23	73.8±1.9
C	B		61.0±4.4
	I		52.6±3.7
	IB F_5	I-48-18	50.6±3.4
	BI F_5	II-53-20	48.6±4.6
	BI F_5	II-53-19	46.8±2.9
	BI F_5	II-53-22	48.2±3.8
	BI F_5	II-22-1	52.0±3.6
	BI F_5	II-22-13	49.6±5.5
	IB F_5	I-26-16	58.8±3.1
	BI F_5	II-50-23	58.6±3.4

†Line No. I-48-18, II-53-20, II-53-19, II-53-22, selected from F_4 the earliest lines for Stage A.
Line No. II-22-1, II-22-13 selected from F_4 the earliest lines for Stage C.
Line No. I-26-16, II-50-23 selected from F_4 the latest lines for Stages A and C.

4. Results of selection in the field experiments

Stage A. As shown in Table 33, the random samples were taken from the F_1 and F_2, and selection for earliness in Stage A was begun in the F_3 in which 6% and 11% were chosen in the IB F_3 and BI F_3 respectively. The IB F_4 mean for earliness was 66.6 days, which was 6 days earlier than B, but 3 days later than I; whereas the BI F_4 mean was 66.8 days, which was 5.9 days earlier than B, and 3.5 days later than I. The earliest of the 10% of the F_4 plants were selected in these reciprocals, and the reciprocal F_5 populations were earlier than both original parents. The IB F_5 was 13.7 days earlier than B and 1.7 days earlier than I, and BI F_5 showed 12.9 days earlier than B, and 1 day earlier than I.

Stage C. Similar selection procedures were used as for Stage A, and the IB F_4 means (Table 34) were 6.5 days earlier than B and 3.1 days later than I; whereas the BI F_4 showed 8.7 days earlier than B and 0.9 days later than I. After the earliest 10% of the F_4 plants were selected, the means for the F_5 progenies were earlier than both parents. The IB F_5 was 10.6 days earlier than B and 2.1 days earlier than I, whereas the BI F_5 was 12.1 days earlier than B and 3.6 days earlier than I.

The means for earliness of the F_5 generation progenies of both reciprocal populations were smaller than the earliest original parent, indicating that there was recombination for earliness between the two stages. In other words, the shortest stages had been brought together in the F_5 reciprocal hybrid populations to produce the early segregants.

TABLE 33: Summary of the field experiments, mean days required for Stage A.

IB F_1	74.6±2.3 random sample taken	BI F_1	74.8±1.5 random sample taken
↓		↓	
IB F_2	75.6±4.8 random sample taken	BI F_2	75.1±4.0 random sample taken
↓		↓	
IB F_3	70.7±7.7 different from B-9.1; I +1.7	BI F_3	72.1±4.0 different from B -8.7; I +3.1
↓	(6% selected)	↓	(11% selected)
IB F_4	66.6±5.7 different from B -6.1; I +3.0	BI F_4	66.8±6.8 different from B -5.9; I +3.5
↓	(10% selected)	↓	(10% selected)
IB F_5	60.3±1.6 different from B -13.7; I -1.7	BI F_5	61.0±4.6 different from B =12.9; I -1.0

TABLE 34: Summary of the field experiments, mean days required for Stage C.

IB F_1	52.3±2.3 random sample taken	BI F_1	51.0±1.0 random sample taken
↓		↓	
IB F_2	49.1±4.6 random sample taken	BI F_2	49.9±4.8 random sample taken
↓		↓	
IB F_3	51.1±5.1 different from B -8.6; I +3.7	BI F_3	49.2±3.5 different from B -10.5; I =1.9
↓	(6% selected)	↓	(11% selected)
IB F_4	49.5±3.4 different from B -6.5; I +3.1	BI F_4	47.3±4.7 different from B -8.7; I =0.9
↓	(10% selected)	↓	(10% selected)
IB F_5	50.5±2.3 different from B -10.6; I -2.1	BI F_5	49.0±6.7 different from B -12.1; I -3.6

DISCUSSION

Diallel Cross Experiments

In the breeding of self-pollinated crop plants, the efficiency depends on accurate identification of the hybrid combinations that have the potential of producing maximum improvement. The present experiments were undertaken to determine whether diallel analysis of parental and F_1 data could provide information useful for producing a maximum earliness.

The data from the diallel cross experiments were subjected to 2 analytical procedures. In the "Hayman and Jinks method" all the assumptions are tested initially by the uniformity of W_r-V_r among arrays. Hayman (1957, 1958) reported that only when the test reveals a lack of uniformity is there need for further tests to investigate which assumption is not valid. One of the common ways is to eliminate certain parental line data and analyze the remaining data again. Due to limited resources for this experiment, there were only 3 parental lines involved; therefore, when data for certain characteristics in the present experiments failed to pass the uniformity test, it was not possible to eliminate a parental line and apply a further test. As shown in Table 5, there were 3 out of 24 characteristics which failed the uniformity test. Nevertheless these 3 partial failures seemed unlikely to introduce gross bias into the total genetic information to be gained from the diallel experiments; therefore, it was assumed that these partial failures would not detract from the total information gained.

According to Hayman (1954), the interaction between ennvironment and the genotype in a diallel cross is revealed by the amount of heterogeneity of the variances within parental and F_1 families. Such heterogeneity may be handled by considering the environmental effects (E) which is estimated from differences between blocks, and subtracted from the genetic parameters, as shown in Table 1. Peat (1964) reported that it is difficult to separate the environmental effect from the genetic effect on certain characteristics, and that using the phenotypic variance will result in a bias. In greenhouse Experiments I and II, there were two negative D values; Stage 2, warm (Table 13) and days required per plastochron, warm (Table 18). These negative values are a result of sample error and also the subtraction of the relatively large environmental effect E from the parental variance, V_p, (i.e. $D=V_p-E$; as shown in Table 1). Since both these characteristics, Stage 2 (from seed germination to first true leaf), and the days required per plastochron (the mean of 3rd to 8th plastochron) both occurred before transplanting to the benches when the distance between seedlings was only 2 inches, then, there was the possibility of competition between the seedlings which may have caused the E value to be so large.

Hayman and Jinks diallel cross theory proposed the use of the parameters F, H_1 and H_2, expecting them to be accurate in a large diallel cross experiment. Hayman (1956) suggested that when the number of parents is less than 10 none of the components of variation in the diallel cross analyses would be significant estimates of population parameters. However, in this experiment, the individual parents and crosses were the main interest, and no attempt was made to

measure the population parameters, thus the genetic information was limited to parental cultivars I, B and C only. The analysis of a diallel cross experiment is somewhat different from the usual analysis of variance because the former estimates the components separately from within each replicate, but the latter from over all replicates.

The value of the numerical method of analysis is that the relative importance of dominance and additive effects and some information on the distribution of alleles within the parental population can be obtained in numerical form, and from these, further estimates such as the degree of dominance can be obtained. In these experiments, the numerical analysis indicated that in the warm regime, overdominance occurred in Stages 1, 2 and 4, partial dominance in Stages 3, 6 and 7, and only Stage 5 showed virtually complete dominance. Previous studies by other workers on earliness did not partition the life cycle into as many component stages as the present work. In general the intensive partitioning results do agree with some of the earlier reports on larger component stages. The present F_1's were usually earlier than the earliest parent in both flowering and fruit set, similar to the reports by Hayes and Jones (1917). Wellington (1922), and Powers and Lyon (1941). The earliness, expressed as days to first flower appears to be a result of overdominance in Stages 1, 2 and 4, and these are a large part of the stage described by Burdick (1954) and Young (1966) who reported that time of flowering in hybrids is approximately intermediate between the two parents and their results would exclude overdominance action. Either their parental types behave differently, or the failure to partition growth component stages

sufficiently prevented them from observing the overdominance as found in Stages 1, 2 and 4 of the present experiments. These stages account for about one half of the time period between germination to flowering, thus the importance of this period for earliness is self-evident. In this experiment Stage 5 showed almost complete dominant gene action which was in agreement with Corbeil (1965) and Corbeil and Butler (1965), who reported that the early maturity genes were completely dominant for the first bloom to first fruit set stage which is the same as Stage 5 in the present study.

In the cool regime, results were quite different. Overdominance for earliness was shown in Stages 1, 5, 6 and 7; partial dominance in Stages 2 and 3, and complete dominance in Stage 4. Comparing the results under the 2 different temperature regimes, the genetic parameters were the same in only Stages 1 and 3 in which there was overdominance and partial dominance respectively, and all other component stages had different gene action. These differences are thus indicated to be due to the genotype-environment interaction.

In the warm regime, the frequency of recessive genes for earliness was higher than dominant genes for Stages 1 and 2, and the opposite way for Stages 3, 4, 5, 6 and 7. The gene number involved in the seven component stages was relatively low, in the warm regime only one or 2 gene pairs exhibited some degree of dominance for Stages 1; 2, 3 and 2 gene pairs for Stages 2, 3 and 4 respectively; and 4 gene pairs for Stages 5, 6 and 7. These results were somewhat different from those of Honma et al. (1963), who reported only one major gene pair for days required from seeding to first flower. In contrast,

Powers et al. (1950) and Fogel and Currence (1950) suggested 3 or more gene pairs controlled this character of earliness of flowering, and the former also reported that 2 major genes appeared to control the stage for fruit set to fruit ripening.

In the cool regime, a larger number of genes appeared to be involved in the earliness of most stages. Comparing the results in Tables 14 and 16, it is seen that in the cool regime, a larger number of genes were involved in each of Stages 1 to 4 inclusive than in the warm regime which represented usual growing conditions for the commercial crop and previous research work. At the later stages, Stage 5 had the same h^2/H_2 value under both regimes, and Stages 6 and 7 had lower values under the cool regime indicating probably one gene pair only showed some measure of dominance. These differences in gene numbers exhibiting some degree of dominance depending on the temperature level are evidence that plant breeders should realize that such responses can be studied in their breeding programmes. Identification of genotypes of special value for cool climates or growing seasons is a problem for the plant breeders "screening procedures" in identifying useful genotypes for providing wider adaptation to less favourable temperature conditions.

The heritabilities for Stages 3 and 6 in the warm regime are high suggesting that selection in the early generations such as the F_2 could be expected to show progress in increased earliness. These two stages are very long components of the life cycle, therefore, they should provide a good opportunity to make progress with earliness. The other stages in the warm regime, and all stages in the cool regime, had lower heritabilities, thus early generation

selection could not be expected to make much progress in the direction of increased earliness.

Greenhouse Experiment II

This experiment contrasted Stages 5 and 6 of the previous greenhouse Experiment I where natural self-pollination occurred, with results of greenhouse Experiment II where pollen was transferred by hand. Although the data for the two experiments show small differences for Stages 5 and 6, these differences were undoubtedly a result of variation in the two seasons, and both experiments showed the same responses when genetic parameters and estimators were calculated. In other words, the differences in earliness as affected by natural or artificial pollination were not large enough to affect the genetic information on earliness. Apparently special pollination handling was not needed, and growth studies can depend on natural pollination to produce a uniform base for plants in their Stage 5. As expected, days required per plastochron, which were recorded from 4th to 8th plastochron, were markedly affected by the temperature regimes. The relationship of the D and H_1 parameters (Table 18) indicated complete dominance for earliness in the warm temperature regime, but overdominance in the cool temperature regime. The gene number involved in this earliness differed with temperature, being 2 and 6 in the warm and cool regimes respectively, and the heritabilities were both very low. Nevertheless it could be important to know the temperature-genotype interactions to aid the plant breeder in choosing breeding procedures; for example, the true-breeding cultivars could be selected for the dominant action for earliness, under warm conditions; however under the stress of cool regimes the use of

F_1 hybrid cultivars could be the desirable choice, particularly to get the overdominance for earliness.

In contrast to the character of earliness, the genetic parameters for the fruit weight and diameter show the same response in both temperature regimes. The smaller size and diameter of fruit of F_1 hybrids compared with the parents (Table 11) were apparently the result of partial dominant gene action (Table 19 and Fig. 21 to 24), and such results are in agreement with the reports of Fogle and Currence (1950) and Kheiralla and Whittington (1962) on tomato fruit size inheritance.

The pictorial analyses, which are genetic analyses using diallel cross graphs (Fig. 1-24), are bases on the value of W_r-V_r. The value of W_r-V_r is equal to $\frac{1}{4}(D-H_1)$ (Hayman, 1954), and must be constant among the arrays to meet the assumption of the diallel cross theory. If the value of $\frac{1}{4}(D-H_1)$ does not change and remains constant, then W_r= constant +V_r, and the regression of W_r upon V_r is a straight line of unit slope. When V_r = 0, then W_r = $\frac{1}{4}(D-H_1)$. Thus on the diallel cross (W_r,V_r) graphs, the intercept on the W_r axis is an indicator of the average degree of dominance in the progeny. With partial dominance, the W_r intercept is positive; with overdominance the W_r intercept is negative. Therefore the (W_r,V_r) graph provides evidence of the presence of dominance ($b \neq 0$) and the average degree of dominance (+ or - value of a). In the present experiment the results of pictorial analyses reveal that the average degree of dominance in all the characters investigated was in agreement with the results of the numerical analyses. Besides this point, the pictorial analyses provide further information which is not obtained from the numerical

procedure. For example, the position of the regression line related to the origin (W_r,V_r) gives a good idea of the degree of dominance; and the position of points along the line reveals the distribution of dominant and recessive alleles within the parental populations. Points near the origin (W_r,V_r) represent parents with mostly dominant alleles, whereas points near the upper end of the regression line represent parents with mostly recessive alleles. From Fig. 1-7, it may be concluded that in the warm temperature regime, the I cultivar carried dominant genes for earliness in all the 7 component stages, and B carried recessive genes which were acting in the direction of lateness. On the other hand, Fig.8-14 show that in the cool temperature regime, I cultivar carried genes for earliness in only Stages 3,4,5 and 6, whereas in Stage 2 dominant earliness was shown by cultivar B; and the dominant earliness for Stages 1 and 7 was manifested by cultivar C. This variation from results in the warm regime could be due to different genotype-environment interactions, and certain genes in certain cultivars were more suitable for growth in the cool temperature environment. It has already been reported (Young, 1963) that C cultivar seed is able to germinate at the cool temperature of 10.0°C and set fruit at 7.5°C night temperature.

From the plant breeder's point of view, the pictorial analysis supplies information about the gene distribution pattern among parents and such information is not obtained in the numerical analyses. In this experiment, cultivar I is desirable for the breeding of earliness, because it carries dominant genes in most of the growth component stages, and these dominant genes are in the direction of earliness.

Additional to the Hayman-Jinks procedure for diallel cross experiments, the Griffing's method was also used, and it is concerned with the general combining ability (G.C.A.) and specific combining ability (S.C.A.). According to Sprague and Tatum (1942) the variance for G.C.A. is largely additive genetic variance, whereas S.C.A. is largely dominance variance. Horner and Lana (1956) indicated that both G.C.A. and S.C.A. contain epistatic variance with the latter containing considerably more than the former.

From the results (Tables 20 and 21), it indicated that in the warm regime, the estimates of variances for G.C.A. were significant atthe 5% level for all 7 component growth stages, indicating the presence of additive gene action. Although significant estimates of S.C.A. were also obtained, when compared to G.C.A., the estimates of non-additive genetic variance (S.C.A.) were generally smaller, especially in Stages 3 and 6. In the cool regime, the estimates of G.C.A. for all the component stages were significant except for Stage 7 whereas the estimates of S.C.A. were all significant. The mean squares of the S.C.A. were larger than those for G.C.A. in Stages 1, 5 and 7 which indicated that non-additive. The significant non-additive gene action should make a recurrent selection more efficient in the early generations if selection is for earliness under a cool regime.

The foregoing demonstrates the contrast in gene action under differing temperature regimes, and choice of breeding methods should obviously be related to the objectives and use of growing conditions for plant breeding programmes.

Considering the days required per plastochron (Table 22) in the warm regime, the G.C.A. and S.C.A. values were both significant whereas in the cool regime, the S.C.A. value was larger than and hence more important than the G.C.A. This high S.C.A. value indicated that this characteristic of earliness can be considered as relatively easily to select and evaluate in a population under selection. This conclusion is similar to that of Khalf-Allah (1970), Khalf-Allah and Peirce (1962), Peirce and Currence (1959), who also reported that the S.C.A. values were larger than those for G.C.A. although their partitioning of the life cycle was different from the present work and did not include plastochrons.

In the warm regime, fruit weight and fruit diameter both had significant values for G.C.A. only (Table 23), whereas in the cool regime both the G.C.A. and S.C.A. were significant. Also under both temperature regimes, the estimates of S.C.A. were both much lower than those for G.C.A. indicating the fruit weight and diameter were largely controlled by additive gene action. This result was not the same as that obtained by Khalf-Allah (1970), who reported that for fruit size, G.C.A. and S.C.A. showed approximately similar values.

Although the same data from the diallel crosses were used in each of two different analytical procedures, the methods are not alternatives, but rather means to extract different genetic information. The Hayman-Jinks method provided several parameters and estimators which were based on data from parents and their F_1 generations, and which could be used as prediction values for selecting among superior lines. Thus a large number of lines could be selected at an early generation, possibly the F_2, and the unpromising lines could be

discarded, allowing breeders to concentrate on a relatively few lines with the expectation of rapid achievment of the breeders' objectives. As already indicated this evaluation procedure might well be adequate for many breeding programmes, including the improvement of earliness in tomatoes.

The second analysis, Griffing's method provided information on the combining abilities of all parental lines in the diallel cross. There is an estimate of the importance of additive and dominant gene action, which may be of great value to the plant breeder when he has to estimate the progeny segregation range in order to decide on the size of the population required, and also to predict the progeny phenotypic values.

As pointed out in the literature review, the Hayman-Jinks technique was concerned with the gene level whereas Griffing's method was concerned with the gametic level. In other words, the Griffing method can be regarded as the combination of gene interactions of the 2 genomes in the zygote. Thus the Griffing's analysis regarded the genotypical effect of an individual as the combination of effects contributed by each gamete and the interaction of gametes, whereas Hayman-Jinks regarded the gene effect which may direct the phenotypic expression. The plant breeder may view the Griffing method as a 'testing' procedure to study and compare the performances of parental lines in hybrid combination, and the Hayman-Jinks method indicates the genetic characteristics of the parental lines.

The plant breeders should keep in mind that there are different contributions from both methods, and ideally any diallel cross experiment should employ both methods to help plant breeders to [illegible] quantitative characters in order to [illegible]

select any quantitative characters in order to achieve the goal.

Reciprocal Cross Experiments

There were different responses in some growth stages in the reciprocal crosses at the 2 temperature regimes in the greenhouses. In the warm regime, there were no significant differences between reciprocals (Table 26) so far as earliness could be measured. Apparently the identical nuclear genes of the reciprocals controlled the growth, and differences in cytoplasm had little if any effect. The responses in the cold temperature regime (Table 26) showed that Stages 1, 3 and 4 were affected by the cytoplasm which parent B contributed, and these stages took longer to develop than in the hybrid where I had contributed the cytoplasm. Although the F_1 hybrids had the same nuclear gene constitution, there is apparently a cytoplasmic-genic interaction such that cytoplasm from B under cool temperatures provides an unsuitable condition for the expression of the genes contributed by both parents to the F_1 reciprocal hybrids. Thus under the stress of cooler conditions, the cytoplasm appeared to have some importance, and this is of particular interest when there is every probability that future greenhouse growers will either wish or be required to produce crops with minimum use of fuel for heating.

The means for earliness for the reciprocals in both temperature regimes in all the stages, with only the one exception of Stage 5, cool, showed a tendency to be closer to the earlier parent I. These results suggest that the nuclear genes were more important in controlling plant growth than the cytoplasmic contribution which was of little importance for growth except under a stress condition. These

results were somewhat different from those of Shumaker et al. (1970), who concluded that most differences between reciprocal F_1's for earliness showed matroclinous tendencies.

Possible cytoplasmic differences could be associated with variation in chlorophyll content as reflected by net photosynthesis rates. The measurement of these rates in the growth chamber Experiment II showed the following trends. Differences in the net photosynthesis rates of parents B and I were not significant until the plants had reached the 6th plastochron and then rates were significantly different through to the 8th plastochron at the end of the experiment (Table 27). This response was similar in both temperature regimes. The reciprocal hybrids showed fewer differences than the parents, and the differences were significant at the 5th and 8th plastochrons in the warm regime and only at the 5th plastochron in the cool regime. The small proportion (3 out of 10 comparisons) of significant differences between reciprocals suggests that the cytoplasmic influences or effects are hardly large enough to concern the plant breeder. It is noted that in spite of the non-significant differences, there is a trend (only one exception out of 10 comparisons) for the I cytoplasm of IB hybrid to be associated with higher net photosynthesis rates than is the case for the reciprocal BI which has the B cytoplasm. This apparently small contribution by the cytoplasm is in general agreement with the evidence presented by Levine (1969), McGinnis and Taylor (1961), Chang and Sadanage (1964) and Izhar and Wallace (1967), who have pointed out that the production of chlorophyll, although located in the cytoplasm, is controlled by nuclear genes.

As shown in Fig. 25 and 26, the net photosynthesis rate for all the lines fluctuated from the 4th to 8th plastochrons. The fluctuation of net photosynthesis rate could be related to the developmental phase of the plant. There are several reports regarding the effects of floral differentiation on photosynthesis rate. Duncan and Hesketh (1968) using corn, Forsyth and Hall (1965) with blueberry, and Richardson (1967) using cotton, all reported that when floral differentiation was occurring, there was a decrease in the net photosynthesis rate. In the tomato when the reproductive phase is underway, there can be retardation in the vegetative growth (Kraus and Kraybill, 1918), and this retardation of vegetative growth may affect the photosynthesis rate, as reported by Sweet and Wareing (1966). In the present experiment, under the warm temperature regime (Fig. 25), the photosynthesis rate decreased in cultivar B from the 5th plastochron, and this decrease may be associated with the floral differentiation which took place from this plastochron age. Similarly the results of the diallel cross in growth chamber Experiment I suggested an association of decreased net photosynthesis rate and floral differentiation in cultivar C.

Considering the leaf area in both temperature regimes, (Table 28), there were differences between the two parents B and I, (I having the smaller leaf area) which were all significant except for the fourth plastochron in the warm regime. None of the differences between reciprocals were significant except those for leaf areas in the 7th and 8th plastochrons in the cool regime, which indicated that the cytoplasmic differences between these two reciprocals

had a slight effect on the leaf area, whereas the significant differences between I vs. IB and B vs. BI indicated the nuclear genes were the major control for leaf area development.

From the results of this reciprocal cross experiment, it may be concluded that under normal growing temperature regimes, the cytoplasmic effect was not as important as the nuclear effect; however, under stress cool temperature conditions, the cytoplasmic effect may reveal some importance especially for the earliness of several growth component stages. It is advisable therefore, that cytoplasmic effects and genic-cytoplasm interactions be studied and carefully considered by plant breeders working on selection for earliness under stress temperature conditions.

Field Selection Experiments

The field Experiments I-III dealt with selection and the search for evidence of recombination among the short growth stages.

Early generation selection and testing have been reported as particularly suitable for evaluating such a crop as the tomato (Khalf-Allah and Peirce, 1964). Peirce and Currence (1959) had concluded that early testing for quantitatively inherited characters, such as earliness, was of definite value in improving tomato plant performance. In the present field experiments, pedigree selection was started in the F_3 for Stages A and C (as defined on page 35) and the top 6% and 11% were selected from reciprocal populations IB and BI respectively. In the F_4 generation, the means for both reciprocal populations did not exceed the mean of the earlier parent I. The heritabilities for the earliness characteristics in the F_4

for both reciprocal populations were relatively high, and higher in Stage A than in Stage C. These heritability differences indicated that Stage A will respond to selection for earliness more efficiently than will Stage C. The theoretically expected selection progress, ΔG, in the IB population was 6.3 days for Stage A and 3.4 days for Stage C (Table 31); whereas in the BI population, these values were 9.6 days for Stage A and 5.4 days for Stage C. These selection progress values do not mean that the following generation will be improved for earliness exactly as calculated, but these values show the relative tendency that, under the selection intensity employed, the population means will be shifted in the expected direction by a certain amount.

In selection work, the genetic progress, σG, is less than selection progress, ΔG, although they are highly correlated with the heritability, h^2, (Pirchner, 1969). In the F_4 generation of the tomato selection experiment (Table 31), the genetic progress was calculated as 4.6 days in Stage A and 2.6 days in Stage C for the IB population; and 6.2 days in Stage A and 3.8 days in Stage C for the BI population. This genetic progress indicated that under the selection intensity employed, the genotypic value for earliness will be changed in the expected direction in the F_5.

Pedigree selection was continued in the F_4 and the top 10% of early plants was selected again from both reciprocal populations. The means of the F_5 mass populations (which were from selected F_4 plants) were earlier than both original parental cultivars (Tables 33 and 34). These earlier F_5 population means indicated that

recombination of some genes for earliness had occurred. Although the means for the F_5 reciprocal populations IB and BI were earlier than original parents I and B, there were differences in the behaviour of reciprocal lines. Within the mass population of IB F_5, the standard deviation was 1.6 for Stage A (Table 33) and 2.3 for Stage C (Table 34), and both these values were smaller than similar values for the F_4 generation, indicating that the segregation in the F_5 of the IB population had been reduced. On the other hand, in the BI population F_5, both the standard deviations for Stages A and C were larger than those for the F_4, and this comparison indicates that segregation was continuing.

Although the F_5 population mean for each of the reciprocal hybrid populations was earlier than the mean of each of the original parents (Tables 33 and 34), the F_5 plants demonstrated that recombination of genes for earliness had occurred. The F_5 reciprocal hybrid populations were apparently not identical. The standard deviation for IB F_5 population in both Stages A and C showed a reduction from the IB F_4 value, however the BI F_5 population had a slightly larger standard deviation than the BI F_4. These standard deviations indicated that the segregation in IB F_5 had been reduced whereas in the BI F_5 segregation was continuing and producing a wider range of segregates. It is suggested that mass selection can be continued in the IB population to maintain or increase the earliness, but pedigree selection should be applied to the BI population to observe further segregations which should allow increased chances for more desirable recombinations for earliness to appear.

The several experiments showed that different cultivars proceeded through various growth component stages at different rates. Genetic parameters and estimators were characteristics which frequently indicated differential genetic behaviour in each of two different temperature regimes, and among these characteristics, high heritabilities were calculated for earliness in the more important or lengthy growth stages. These characteristics were used to choose parental lines and to employ early generation selection. The F_4 generation selection in two reciprocal cross populations provided a good example of the results of early generation selection to obtain recombination of genes from two parents to produce plants (in F_5) which had the shortest growth Stages A and C and which were earlier than either parent.

This increased earliness of some recombinations provides an example of the potential success to be gained from using shorter component stages from many different parental cultivars to obtain recombinations which would achieve the objective of breeding for earliness to adapt the tomato to short and cool growing seasons in Canada.

SUMMARY

The inheritance of 7 growth component stages and other physiological characteristics in tomatoes was studied in (a) diallel crosses among 3 cultivars, Bonny Best, Immur Prior Beta and Cold Set; and (b) reciprocal crosses between 2 cultivars, I and B. These experiments were conducted in 2 temperature regimes, 10-13°C and 17-21°C. Selection was applied starting in the F_3 through to the F_5 in the field, to seek evidence of genetic recombination between component stages and the response to selection for the earliness.

Data on growth stages from the diallel crosses were subjected to 2 analytical procedures. The first procedure used the Jinks and Hayman (1953) model to provide parameters and estimators which indicated gene action in the several growth stages. The action revealed varied among the 7 stages and between the 2 temperature regimes. Stages differed as to whether overdominance, partial or complete dominance was present. The dominant and recessive allele frequencies were not equal in any stages and varied in different stages. The heritability for earliness of most stages was relatively high. Temperature had considerable effect on the action.

The second procedure, Griffing's method (1956), provided an estimate of the General Combining Ability and Specific Combining Ability, and their values differed significantly in different stages and also in different temperature regimes indicating that both additive and dominant gene action were important in most of the component stages, although the temperature regimes affected this action such

that in some stages in the cool regime, the dominant action was more evident.

The reciprocal cross experiments showed that although parents had significant differences in most of the component stages in both temperature regimes, their reciprocal cross progeny showed no significant differences among any of the component stages in the warm regime, but showed significant differences in Stages 1, 3 and 4 in the cool regime. Thus cytoplasmic differences appeared to have some importance under the stress of the cool regime.

The net photosynthesis rate in parents I and B showed significant differences in plastochron ages 6 to 8 inclusively, but the reciprocal progenies showed significant differences at the 5th and 8th in the warm regime and only at the 5th in the cool regime.

The differences in some of the genetic parameters and estimators in the 2 temperature regimes in the diallel crosses, and the differences between reciprocal crosses, provide knowledge to aid the plant breeder to choose breeding procedures for improving the quantitative characters including appropriate testing procedures to identify valuable segregants. The demonstrated effects of temperature on gene action make it important that the environmental factor be carefully considered in the breeding programme.

Three seasons of field experiments were used to select for earliness in growth Stages A (seeding to first flower) and C (fruit set to ripening). Selection was done in the F_3, in 2 reciprocal cross populations, IB and BI. The F_4 progenies from the selected plant had means for earliness which were intermediate between the parents I and B, with a consistent tendency to be closer to the

earlier parent. Selection was continued in the F_4, and the means for the F_5 reciprocal populations were earlier than the original parents. This F_5 response must have resulted from favourable recombinations of genes for the quantitative characteristics of earliness in the 2 component growth stages of the original parents.

Further progress in increasing the earliness characteristic should be possible if further component growth stages are studied and recombinations of shortest stages are continued, but different responses and results may be influenced by choice of temperature regimes.

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APPENDIX

List of Appendix Tables

Page

Table 1. Experimental design for the greenhouse experiment I.

Block 1	CB	BC	I	IB	C	B	CI	BI	IC
Block 2	BC	I	IC	CI	B	BI	C	IB	CB
Block 3	B	CI	BC	CB	IB	I	BI	IC	C
Block 4	C	BC	CB	I	BI	CI	B	IB	IC

Table 2. Temperature record during the greenhouse experiment I.

date	warm	cool
Oct.26-Nov.3	17.2	10.0
Nov.3-Nov.10	18.3	10.6
Nov.10-Nov.17	17.8	13.3
Nov.17-Nov.24	17.2	13.9
Nov.24-Dec.1	17.2	13.9
Dec.1-Dec.8	17.2	12.8
Dec.8-Dec.15	17.2	12.8
Dec.15-Dec.22	17.8	12.8
Dec.22-Dec.29	17.2	12.8
Dec.29-Jan.5	17.2	13.9
Jan.5-Jan.12	17.8	13.3
Jan.12-Jan.19	17.2	12.8
Jan.19-Jan.26	17.2	13.3
Jan.26-Feb.2	16.7	12.8
Feb.2-Feb.9	16.1	11.7
Feb.9-Feb.16	16.1	11.7
Feb.16-Feb.23	16.1	11.7
Feb.23-Mar.2	16.7	12.8
Mar.2-Mar.9	16.7	12.2
Mar.9-Mar.16		12.8
Mar.16-Mar.23		12.8
Mar.23-Mar.30		12.8
Mar.30-Apr.6		12.8
Apr.6-Apr.13		12.8
Apr.13-Apr.20		12.8
Apr.20-Apr.27		12.8

average temperature daily, °C.

Table 3. Experimental design for the greenhouse experiment II.

Block 1	CI	B	IC	IB	C	CB	BI	BC	I
Block 2	C	IB	I	BI	B	CB	IC	BC	CI
Block 3	C	B	BC	CI	BI	IC	I	CB	IB
Block 4	CB	C	I	IB	BC	B	CI	BI	IC

Table 4. Temperature record during the greenhouse experiment II.

date	warm	cool
Nov.1-Nov.8	16.7	12.8
Nov.8-Nov.15	17.2	12.8
Nov.15-Nov.22	17.8	12.2
Nov.22-Nov.29	17.8	12.2
Nov.29-Dec.7	17.8	12.8
Dec.7-Dec.14	17.8	12.8
Dec. 14-Dec. 21	20.0	14.4
Dec. 21-Dec.28	18.3	11.1
Dec.28-Jan.4	17.8	13.3
Jan.4-Jan.11	18.9	12.2
Jan.11-Jan.18	17.8	12.2
Jan.18-Jan.25	18.9	12.2
Jan.25-Feb.1	17.8	12.2
Feb.1-Feb.8	17.2	13.3
Feb.8-Feb.15	17.8	12.2
Feb.15-Feb.22	17.2	12.2
Feb.22-Mar.1	17.8	11.7
Mar.1-Mar.8	17.8	11.1
Mar.8-Mar.15	17.8	12.2
Mar.15-Mar.22	16.7	11.7
Mar.22-Mar.29		13.3
Mar.29-Apr.5		12.8
Apr.5-Apr.12		12.8
Apr.12-Apr.19		12.8

average temperature daily, ^{o}C.

Table 5. Experimental design for the greenhouse experiment III.

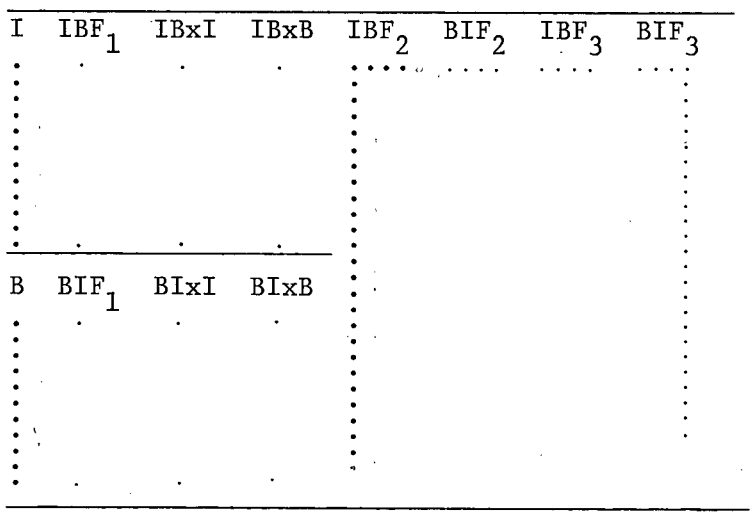
Block 1		Block 2		Block 3		Block 4		Block 5	
I	B	I	IB	BI	I	B	BI	IB	B
BI	IB	BI	B	B	IB	I	IB	I	BI
Block 6		**Block 7**		**Block 8**		**Block 9**		**Block 10**	
B	BI	BI	IB	I	B	IB	I	I	BI
I	IB	I	B	BI	IB	BI	B	B	IB

Table 6. Temperature record during the greenhouse experiment III.

date	warm	cool
Oct.29-Nov.8	21.1	15.6
Nov.8-Nov.15	21.7	15.6
Nov.15-Nov.22	20.0	16.1
Nov.22-Nov.29	18.3	12.8
Nov.29-Dec.6	17.8	14.4
Dec.6-Dec.13	17.8	12.2
Dec.13-Dec.20	17.8	13.9
Dec.20-Dec.27	17.2	12.2
Dec.27-Jan.3	17.2	12.2
Jan.3-Jan.10	17.2	12.2
Jan.10-Jan.17	17.8	11.7
Jan.17-Jan.24	17.2	13.9
Jan.24-Jan.31	16.7	11.7
Jan.31-Feb.7	17.2	11.1
Feb.7-Feb.14	17.8	11.7
Feb.14-Feb.21	17.2	12.2
Feb.21-Feb.28	16.1	12.2
Feb.28-Mar.6	16.7	11.1
Mar.6-Mar.13	16.7	12.8
Mar.13-Mar.20		13.9
Mar.20-Mar.27		12.2
Mar.27-Apr.3		13.3
Apr.3-Apr.10		13.3
Apr.10-Apr.17		13.3
Apr.17-Apr.24		12.8
Apr.24-May.1		12.8
May 1-May 6		16.7

average temperature daily, ^{o}C.

Table 7. Planting plan for the field experiment I.



Every '.' represents one plant

Table 8. Experimental design for the field experiment II.

Block	plant	plot 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	1	II-2	I-11	II-35	IPB	II-4	I-51	II-10	I-12	II-50	B	I-26	II-25	II-19	II-22	II-33	I-33	II-53	II-53	I-48	II-16
	2																			
	3																			
	4																			
	5																			
2	1	II-16	II-35	I-12	II-50	II-2	II-25	II-33	II-19	I-48	B	II-22	I-33	II-53	II-10	I-26	II-4	IPB	IPB	I-51	I-11
	2																			
	3																			
	4																			
	5																			
3	1	II-53	II-2	II-25	I-48	II-33	I-26	II-22	II-4	II-16	I-11	II-10	II-50	I-51	II-35	IPB	I-12	B	I-33	II-19
	2																			
	3																			
	4																			
	5																			
4	1	II-33	I-48	II-25	I-26	II-53	II-50	I-11	II-10	IPB	I-33	II-35	II-16	I-12	II-19	I-51	B	II-2	II-22	II-4
	2																			
	3																			
	4																			
	5																			
5	1	I-26	II-33	II-53	I-48	II-10	I-12	II-25	II-4	II-19	I-33	IPB	II-2	I-51	II-22	II-35	I-11	II-50	II-16	B
	2																			
	3																			
	4																			
	5																			

'I' from IBF_3; 'II' from BIF_3

Table 9. Planting plan for the field experiment III.

Rep.	Line										
	IB F_5	IPB	BB	BI F_5	F_5-1	F_5-2	F_5-3	F_5-4	F_5-5	F_5-6	F_5-7	F_5-8
1	.....	.	.	.....	.	.	.	.	.	.	.	.
2	:			:	:	:	:	:	:	:	:	:
3	:			:	:	:	:	:	:	:	:	:
4	:			:	:	:	:	:	:	:	:	:
5	:			:	:	:	:	:	:	:	:	:
	.....			.....								

every '.' represents one plant

Table 10. Days required for the 7 stages in the greenhouse experiment I in the warm regime.

Male parent	Stage	Female parent											
		B				I				C			
		Replicate											
		1	2	3	4	1	2	3	4	1	2	3	4
B	1	9.5	8.8	8.7	7.9	7.0	6.3	6.4	6.3	7.0	6.9	7.1	6.4
	2	9.2	9.4	9.1	9.0	8.3	8.6	8.5	8.5	11.7	11.5	11.5	11.5
	3	33.8	34.6	31.9	30.0	22.6	22.3	23.4	21.4	20.8	23.0	19.0	18.0
	4	21.0	23.0	23.0	20.0	21.0	21.0	20.0	23.0	19.0	17.0	16.0	19.0
	5	9.1	9.0	9.3	8.6	6.4	6.2	6.5	6.6	8.5	6.7	7.1	6.5
	6	44.8	45.0	43.7	45.6	37.0	38.1	37.2	38.4	45.5	43.3	43.7	44.2
	7	7.2	6.0	7.0	6.8	5.4	4.8	5.2	5.5	5.0	5.1	5.6	5.3
I	1	7.3	6.5	6.6	7.4	7.6	7.3	6.8	7.5	6.3	6.3	6.7	6.0
	2	8.7	9.4	9.4	9.0	9.0	8.7	9.2	9.0	10.2	10.0	10.1	9.9
	3	20.2	22.5	19.5	23.9	18.0	17.3	15.8	18.0	19.6	18.8	17.7	18.5
	4	17.0	20.0	21.0	23.0	19.0	17.0	19.0	19.0	17.0	18.0	17.0	19.0
	5	6.6	5.7	6.4	5.2	6.4	6.8	6.0	6.8	6.8	6.8	6.4	6.6
	6	38.3	41.1	41.0	42.4	37.0	34.2	36.1	35.9	40.5	40.0	39.8	38.9
	7	4.8	5.3	5.0	5.2	4.7	5.2	4.9	5.0	4.9	4.9	5.2	5.0
C	1	8.0	6.3	7.6	7.0	6.0	6.4	6.3	7.0	7.8	7.0	7.3	7.5
	2	9.0	8.5	8.6	8.5	9.8	9.8	11.3	9.9	9.2	9.3	9.1	9.2
	3	24.2	22.7	20.6	20.0	21.8	19.7	19.2	19.7	22.8	21.7	21.9	21.8
	4	25.0	20.0	18.0	20.0	17.0	17.0	17.0	17.0	27.0	20.0	23.0	21.0
	5	8.4	7.5	8.5	7.8	5.6	6.3	6.4	6.5	8.6	6.3	6.7	8.0
	6	45.5	46.3	46.0	45.7	37.8	39.8	41.2	40.5	45.7	48.3	49.8	48.1
	7	5.0	5.8	5.3	6.2	4.4	5.1	5.4	4.9	5.1	5.3	5.7	5.4

Table 11. Days required for the 7 stages in the greenhouse experiment I in the cool regime.

Male parent	Stage	Female parent: B, Replicate 1	B, 2	B, 3	B, 4	I, 1	I, 2	I, 3	I, 4	C, 1	C, 2	C, 3	C, 4
B	1	17.9	19.0	18.3	18.7	14.4	15.0	15.0	15.5	15.9	15.0	14.1	14.3
	2	9.5	9.2	9.6	9.8	7.6	7.9	8.6	9.3	10.0	10.0	10.4	12.1
	3	38.5	37.8	35.4	35.0	25.4	24.1	23.4	20.7	31.0	29.0	27.6	26.9
	4	72.0	71.0	70.0	70.0	60.0	58.0	60.0	59.0	50.0	53.0	54.0	54.0
	5	23.2	22.6	22.9	23.0	17.3	18.9	17.2	17.0	18.0	18.0	18.2	18.1
	6	62.7	64.5	64.7	63.8	46.2	44.5	45.2	44.0	63.8	64.9	65.0	64.7
	7	10.0	9.8	9.6	9.9	6.8	7.2	6.7	6.8	7.3	7.0	7.5	7.5
I	1	15.0	14.7	15.5	15.3	16.7	16.0	16.3	16.3	16.9	16.4	15.1	14.4
	2	9.4	8.5	8.5	8.0	10.0	9.4	9.3	9.3	10.7	11.1	10.7	10.6
	3	23.3	25.1	20.1	24.6	19.5	19.7	21.2	19.8	20.1	19.8	18.9	19.4
	4	49.0	52.0	53.0	51.0	58.0	59.0	58.0	57.0	46.0	50.0	47.0	47.0
	5	18.6	19.0	18.9	18.7	21.0	20.0	20.8	18.1	19.3	18.9	19.0	18.8
	6	43.2	40.8	42.6	42.9	48.2	48.7	49.5	49.2	59.2	57.6	58.7	56.9
	7	7.6	7.2	7.9	7.5	7.0	6.8	8.2	8.0	9.6	10.0	8.9	10.0
C	1	17.7	17.3	15.5	15.0	15.9	16.3	15.0	16.0	15.7	16.0	14.9	16.4
	2	9.4	7.0	9.6	9.7	12.0	11.2	10.9	10.6	12.2	12.4	12.4	12.5
	3	29.4	20.8	27.2	27.1	19.0	19.1	18.9	18.2	28.1	26.9	26.8	24.9
	4	52.0	53.0	52.0	54.0	58.0	60.0	57.0	62.0	50.0	52.0	54.0	51.0
	5	17.8	18.0	18.1	17.9	71.0	18.6	17.8	18.0	17.9	18.0	18.6	18.7
	6	64.1	65.0	64.7	65.2	58.0	62.0	56.2	57.8	52.7	53.2	52.6	53.4
	7	7.2	6.9	7.0	7.3	8.6	9.2	8.2	9.0	8.1	8.6	8.0	8.4

Table 12. Days required for stages 5 and 6 in the greenhouse experiment II in the warm regime.

Male parent	Stage	Female parent											
		B				I				C			
		Replicate											
		1	2	3	4	1	2	3	4	1	2	3	4
B	5	8.0	8.0	8.0	8.0	7.0	6.0	6.0	6.0	6.5	6.5	7.0	7.0
	6	37.0	39.0	40.0	44.0	34.5	33.5	37.0	36.0	41.0	44.5	41.5	43.0
I	5	6.0	7.0	5.5	6.0	7.0	6.0	6.5	5.5	6.0	7.0	6.0	7.0
	6	33.5	35.0	33.0	36.0	31.0	35.0	32.0	28.0	37.0	35.0	35.0	38.5
C	5	8.0	8.5	8.0	7.5	5.5	6.5	7.0	7.0	5.5	7.0	6.0	6.0
	6	41.0	36.5	38.0	39.5	34.5	35.5	39.0	39.0	44.5	42.5	40.5	46.0

Table 13. Days required for stages 5 and 6 in the greenhouse experiment II in the cool regime.

Male parent	Stage	Female parent											
		B				I				C			
		Replicate											
		1	2	3	4	1	2	3	4	1	2	3	4
B	5	7.0	7.0	6.5	6.0	8.0	9.0	7.5	7.0	7.5	9.0	8.0	7.0
	6	60.0	58.0	56.5	60.0	53.0	48.5	49.5	60.0	62.5	62.0	64.0	63.0
I	5	8.0	7.0	8.0	7.0	9.0	10.0	9.0	9.0	11.0	8.5	7.0	8.0
	6	54.0	54.0	54.0	55.0	51.0	50.5	55.5	53.0	56.0	50.0	59.5	56.0
C	5	7.5	9.0	7.0	7.0	11.0	10.0	9.5	9.5	7.5	7.5	8.0	7.0
	6	63.5	63.0	68.0	65.0	58.0	57.0	59.5	58.5	55.5	57.0	58.5	60.0

Table 14. Days required per plastochron in the greenhouse experiment II in the warm regime.

Male parent	Stage	Female parent											
		B				I				C			
		Replicate											
		1	2	3	4	1	2	3	4	1	2	3	4
B	1	4.5	4.4	4.4	4.3	3.7	3.7	3.8	3.7	4.0	4.0	4.1	4.2
I		3.5	3.7	3.7	3.7	3.7	3.8	3.8	3.8	4.1	4.0	4.1	4.1
C		4.0	3.7	4.0	3.8	3.9	3.7	4.0	4.0	4.0	4.0	4.1	4.2

Table 15. Days required per plastochron in the greenhouse experiment II in the cool regime.

Male parent	Female parent											
	B				I				C			
	Replicate											
	1	2	3	4	1	2	3	4	1	2	3	4
B	5.9	5.9	6.0	6.1	5.4	5.9	6.1	6.1	5.4	5.3	5.5	5.6
I	5.4	5.4	5.1	5.3	6.0	5.9	5.9	5.9	5.9	5.9	5.6	5.5
C	5.8	5.7	6.2	6.1	5.9	5.8	5.5	5.7	6.5	6.4	6.0	6.1

Table 16. Fruit weight (g) and fruit diameter (mm) in the greenhouse experiment II under two temperature regimes.

Line	Block	Temperature			
		warm		cool	
		Characteristics			
		fruit weight	fruit diameter	fruit weight	fruit diameter
B	1	89.5	53.5	195.3	70.0
	2	102.5	58.0	200.2	76.0
	3	93.5	56.0	186.7	68.0
	4	85.6	56.0	227.8	78.0
I	1	22.1	34.0	27.0	37.0
	2	28.4	36.5	27.9	37.5
	3	18.2	31.5	26.2	35.5
	4	18.0	33.5	32.8	40.0
BI	1	33.3	40.0	72.9	46.0
	2	47.2	44.5	44.9	44.0
	3	43.1	44.0	45.6	45.0
	4	33.5	39.5	46.0	46.8
IB	1	21.7	34.0	57.6	47.0
	2	37.3	41.0	57.5	48.0
	3	52.9	48.0	59.9	48.0
	4	39.0	41.0	75.0	52.5
C	1	47.4	45.5	80.5	53.5
	2	72.6	51.5	78.5	53.0
	3	67.0	48.5	80.0	53.0
	4	120.0	63.0	78.5	52.0
BC	1	112.1	59.5	92.6	57.0
	2	91.0	55.0	90.3	55.0
	3	100.0	57.0	96.7	58.0
	4	95.3	57.0	86.5	55.0
CB	1	94.3	58.0	95.0	53.0
	2	111.5	65.0	100.2	58.0
	3	50.3	44.0	101.0	58.0
	4	65.2	50.0	97.3	54.0
IC	1	25.0	36.5	58.7	49.0
	2	44.3	42.5	49.4	45.0
	3	33.7	38.0	58.0	49.0
	4	48.0	45.0	39.9	41.5
CI	1	34.2	40.5	63.0	48.0
	2	47.5	45.0	44.9	48.0
	3	31.9	39.0	60.2	49.0
	4	48.5	45.0	52.9	46.0

Table 17. Days required for stages in the greenhouse experiment III in the warm regime.

Line	Stage	Replicate									
		1	2	3	4	5	6	7	8	9	10
B	1	9	8	8	8	8	9	8	8	8	8
	2	8	8	8	8	8	8	7	8	8	8
	3	31	32	32	32	33	34	33	32	31	31
	4	36	34	36	34	32	33	31	31	31	30
	5	7	6	7	7	6	8	8	8	8	7
	6	31	32	31	31	38	41	35	35	42	40
	7	9	8	9	10	8	17	9	10	7	7
I	1	8	7	8	7	7	7	7	7	7	7
	2	6	7	7	7	6	6	6	6	7	6
	3	21	20	19	19	18	18	18	19	19	19
	4	25	25	27	22	22	23	22	24	22	31
	5	5	6	6	8	6	7	7	7	7	5
	6	25	30	29	28	29	35	27	38	27	36
	7	6	6	5	5	5	5	7	5	6	6
BI	1	8	7	8	7	7	7	7	7	7	7
	2	6	7	7	6	7	7	7	7	6	7
	3	25	24	23	25	22	25	24	25	25	25
	4	25	25	26	26	25	24	24	25	24	25
	5	6	8	8	7	7	10	7	6	5	6
	6	41	27	28	30	32	40	32	27	39	30
	7	7	6	5	5	4	7	6	5	5	5
IB	1	7	8	8	7	7	7	7	7	7	7
	2	7	6	7	7	7	7	8	7	7	7
	3	27	27	29	27	24	23	28	26	24	25
	4	23	23	24	24	25	24	24	24	24	24
	5	6	8	5	5	6	7	6	7	6	7
	6	29	27	32	30	29	36	28	29	32	30
	7	5	4	4	5	6	5	6	6	6	6

Table 18. Days required for stages in the greenhouse experiment III in the cool regime.

Line	Stage	Replicates									
		1	2	3	4	5	6	7	8	9	10
	1	19	21	20	21	20	20	20	20	20	20
	2	9	9	9	10	11	10	10	10	9	10
	3	28	30	29	30	32	30	34	31	34	34
B	4	65	65	66	63	64	64	64	66	67	66
	5	8	10	7	8	11	10	10	9	11	11
	6	59	60	59	59	60	61	61	60	59	59
	7	11	9	11	12	9	8	7	9	11	8
	1	18	18	16	16	17	17	17	17	17	17
	2	10	9	9	9	9	8	10	10	9	9
	3	20	18	19	19	20	19	19	19	22	18
I	4	49	51	51	50	53	47	47	55	51	44
	5	9	8	11	10	8	10	10	12	12	12
	6	52	53	53	51	53	54	54	52	48	47
	7	9	8	11	10	8	8	7	9	13	14
	1	18	18	16	17	17	17	17	17	17	17
	2	9	8	8	8	9	8	9	10	9	8
	3	26	25	26	24	26	24	25	26	25	27
BI	4	49	52	50	51	50	50	49	50	56	50
	5	8	8	9	9	10	9	8	11	10	9
	6	40	41	41	43	42	40	42	43	41	40
	7	8	8	9	15	9	9	9	8	9	10
	1	19	17	18	19	18	18	18	18	18	18
	2	7	8	8	9	9	8	7	7	8	9
	3	30	28	28	28	28	30	27	29	28	29
IB	4	58	59	58	57	56	56	57	58	57	57
	5	8	9	8	7	8	10	9	9	10	10
	6	50	44	44	49	41	38	42	42	41	40
	7	7	9	7	10	8	7	9	9	9	10

Table 19. Net photosynthesis rate ($mgCO_2/dm^2/hr$) in the growth chamber experiment II in the warm regime.

Line	Rep.	Plastochron 4	5	6	7	8
B	1	9.91	14.57	11.31	11.88	8.40
	2	10.38	15.51	10.94	10.50	7.69
	3	11.07	16.23	11.08	11.27	8.12
	4	11.09	17.23	10.20	8.78	8.97
I	1	11.61	14.08	5.65	19.15	9.67
	2	13.41	15.36	5.91	18.38	8.71
	3	12.89	14.20	5.12	20.79	9.88
	4	12.96	15.02	7.73	23.47	9.49
IB	1	18.59	15.50	11.71	10.46	8.22
	2	16.19	17.30	10.78	12.76	7.94
	3	17.54	14.60	11.02	9.13	8.96
	4	16.31	18.59	11.24	10.28	8.33
BI	1	17.61	13.97	10.44	6.07	6.75
	2	15.59	13.38	8.55	6.99	5.65
	3	14.51	14.41	8.74	7.49	6.87
	4	17.65	14.21	9.97	9.25	6.56

Table 20. Leaf area (cm^2) in the growth chamber experiment II in the warm regime.

Line	Rep.	Plastochron 4	5	6	7	8
B	1	57	85	161	236	356
	2	68	91	151	233	375
	3	54	101	142	252	382
	4	70	105	162	249	380
I	1	51	64	89	152	286
	2	50	64	97	174	289
	3	52	75	96	175	271
	4	49	60	106	155	290
IB	1	46	85	140	247	383
	2	39	90	152	226	389
	3	44	101	157	249	395
	4	43	97	140	238	400
BI	1	49	88	128	259	414
	2	43	98	133	250	404
	3	51	91	150	239	401
	4	46	98	148	260	396

Table 21. Net photosynthesis rate ($mgCO_2/dm^2/hr$) in the growth chamber experiment II in the cool regime.

Line	Rep.	Plastochron 4	5	6	7	8
	1	9.82	7.20	6.32	11.64	5.82
	2	8.93	8.62	4.42	10.31	6.90
B	3	10.21	8.93	6.75	10.02	4.21
	4	10.50	10.10	5.28	9.82	5.69
	1	9.40	9.47	12.50	6.12	9.06
	2	10.19	8.51	10.84	5.49	8.38
I	3	8.29	8.81	12.17	4.05	6.73
	4	8.29	9.80	12.07	5.77	7.46
	1	10.91	13.60	10.25	8.67	4.44
	2	11.11	13.17	13.02	7.75	3.71
IB	3	9.89	12.97	11.43	7.01	5.67
	4	12.57	14.11	10.50	6.12	5.53
	1	10.13	10.33	9.56	7.91	3.02
	2	11.23	9.82	10.80	6.69	3.72
BI	3	9.76	8.02	11.25	9.82	3.15
	4	10.10	10.58	11.91	8.30	3.52

Table 22. Leaf area (cm^2) in the growth chamber experiment II in the cool regime.

Line	Rep.	Plastochron 4	5	6	7	8
	1	64	114	159	188	220
	2	56	116	176	186	215
B	3	58	112	170	183	209
	4	52	115	162	190	211
	1	34	88	112	153	184
	2	36	75	120	170	192
I	3	33	82	115	173	189
	4	44	109	116	165	190
	1	50	92	159	205	246
	2	46	95	169	200	237
IB	3	55	90	140	195	240
	4	58	89	153	190	245
	1	69	88	157	216	272
	2	65	96	137	218	269
BI	3	52	104	160	232	275
	4	54	106	168	230	280

Table 23. Days required for stages A and C in the field experiment I, part 1.

Stage	Rep.	Line I	B	IB)F_1	BI)F_1	IBxI	BIxI	IBxB	BIxB
	1	72	82	74	77	70	72	77	82
	2	70	82	74	75	69	73	78	81
	3	70	79	74	74	68	70	73	72
	4	70	77	74	75	71	71	76	79
	5	70	81	75	76	68	71	77	86
A	6	71	82	80	77	72	71	76	79
	7	67	80	74	72	67	71	77	79
	8	69	80	71	74	71	72	82	80
	9	65	80	73	73	71	71	76	80
	10	71	82	73	74	66	73	76	83
	11	64	82	77	71	69	74	75	76
	12	68	82	74	75	70	68	78	78
	1	47	56	53	51	47	50	52	55
	2	46	56	46	51	47	47	52	51
	3	45	58	52	52	51	47	56	51
	4	41	60	54	50	47	50	56	59
	5	41	58	54	51	48	50	57	55
C	6	47	57	50	49	48	51	53	55
	7	47	59	54	52	48	52	59	60
	8	52	62	53	52	46	53	45	54
	9	53	62	53	51	48	52	50	56
	10	48	63	53	50	49	49	54	57
	11	50	63	53	51	53	52	52	57
	12	50	62	52	52	48	53	53	54
mean		68.9							

Table 24. Days required for stages A and C in the field experiment II.

Stage	Line	Line No.	Block 1	2	3	4	5	mean
A	B		72.2	72.4	74.4	71.8	72.6	72.7±1.7
	I		63.6	63.2	63.0	63.4	63.4	63.3±0.5
	IB F_4	I-11	69.8	71.4	69.6	69.4	71.6	66.6±5.7
		I-12	72.8	61.8	70.3	70.4	63.0	
		I-26	63.6	62.8	64.4	63.4	62.4	
		I-33	63.8	64.0	67.6	64.8	66.2	
		I-48	73.4	68.6	57.4	64.2	61.6	
		I-51	68.2	67.2	67.4	68.6	68.2	
	BI F_4	II-2	62.8	64.4	66.2	72.3	65.8	66.8±6.8
		II-4	68.8	66.0	66.6	64.8	67.0	
		II-10	63.8	69.6	66.2	64.8	62.6	
		II-16	71.3	73.2	72.0	75.0	70.4	
		II-19	63.4	66.0	67.3	67.8	66.2	
		II-22	64.2	67.2	63.2	73.2	69.0	
		II-25	68.6	66.8	67.4	64.8	69.0	
		II-33	67.6	68.6	68.0	68.6	68.6	
		II-35	64.8	65.8	66.0	67.2	66.0	
		II-50	64.8	66.4	74.2	65.8	65.2	
		II-53	63.4	61.8	62.4	58.6	61.0	
C	B		54.0	56.0	56.4	57.8	55.6	56.0±3.1
	I		44.8	47.0	48.0	45.4	46.8	46.4±2.9
	IB F_4	I-11	52.2	49.8	51.2	51.4	49.4	49.5±3.4
		I-12	43.6	47.0	48.4	51.8	46.6	
		I-26	48.0	51.0	46.8	45.2	48.6	
		I-33	46.6	53.6	47.8	48.8	47.0	
		I-48	52.8	52.2	49.2	46.2	48.8	
		I-51	50.0	55.0	54.6	47.2	53.4	
	BI F_4	II-2	51.6	48.8	50.4	48.9	50.0	47.3±4.7
		II-4	45.4	54.2	47.6	48.2	45.4	
		II-10	51.4	54.4	51.8	46.2	57.4	
		II-16	43.8	47.2	51.2	46.4	50.0	
		II-19	52.0	42.0	48.6	46.4	45.2	
		II-22	41.8	45.8	44.6	48.0	50.0	
		II-25	40.6	49.6	42.2	50.6	47.0	
		II-33	52.7	45.6	49.0	46.4	53.0	
		II-35	43.2	45.8	49.6	47.4	44.6	
		II-50	41.2	42.2	49.0	41.6	44.4	
		II-53	43.2	46.2	46.6	43.4	42.8	

each datum is the mean of the 5 plants.