QUANTITATIVE INHERITANCE STUDIES OF GRAIN MATURATION AND GERMINATION IN THREE WHEAT CROSSES.

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ABSTRACT

The pattern of grain maturation and germinability was studied in three wheat crosses ripening in warm and cool environments. Two white grained and two red grained wheat cultivars with varying resistance to preharvest sprouting were used as parents in three crosses. The white grained wheats were Tordo, "resistant" to sprouting through gibberellin insensitivity,and Gabo, a standard cultivar susceptible to sprouting. The two red grained wheats were Karamu and Sonora 64A, the former being sprouting resistant while the latter was susceptible. Tordo was the common parent in all three crosses. Six generations, P_1, P_2, F_2, F_3, $BC_1(P_1)S_1$ and $BC_1(P_2)S1$ from each cross were grown in a glasshouse and were transferred into controlled climate rooms at booting stage, being arranged in a randomized complete block experiment with three replications. The patterns of grain development were measured from serial samples of the grains from ears which had been tagged at anthesis. The changes in grain dry weight, moisture content, germination and α-amylase activities were measured at intervals from just after anthesis until maturity; and the patterns were described using regression analysis against age of grain (in days after anthesis). The functions of best fitted were used to estimate nine key stages of grain development, which were : harvest ripeness, amylase maturity, GA amylase maturity, median germination, germination maturity, median embryo maturity, embryo maturity, grain colour maturity and grain weight maturity.

Gene effects were estimated for these variables, and also for maximum grain coat colour, grain weight at harvest ripeness, maximum dry weight, α-amylase activities at harvest ripeness and at embryo maturity, standard germination and potential germination at harvest ripeness. The gene effects were fitted using Hayman's Generation Means Analysis. The full twelve parameter model (digenic epistasis, environment and their interactions included) were used to explain the

phenotypic variations among the six genetic populations ripening in the two environments. The gene effects estimated were used to assist in making recommendation for breeding for preharvest sprouting resistance.

The experimental results showed that cool environment prolonged the time to reach most developmental stages compared to the warm environment. Harvest ripeness (12.5 % grain moisture) occurred after grain weight maturity (time to 90 % maximum grain weight) but before the time when the grains reached their maximum dry weight. Embryo maturity, as a measure of ability of the grains to germinate when the dormancy had been bypassed, was considered the important component for germinability. Germinative α-amylase at harvest ripeness was the variable most consistently correlated with germination at harvest ripeness.

The gene actions for the derived variables appeared to be complicated, with epistasis and epistasis x environment effects being significant more often than the additive or dominance effects. The gene actions for the maximum grain colour and percent sterility were also studied. For the maximum colour score the result indicated that there was interallelic interaction between the "classical" gene for grain redness and unknown genes. The breeding strategies for preharvest sprouting resistance were discussed based on the actions of the genes for the characters. Briefly it appeared that producing hybrids would enhance the earliness in many maturity characters which would indirectly resulted in more susceptible genotypes. To improve resistance to preharvest sprouting, selection for characters like low α-amylase activities at harvest ripeness, low standard germination and potential germination at harvest ripeness, or late embryo maturity was recommended. These characters were controlled by many genes which interacted and showed epistasis effect and also the gene effects were dependent on environmental condition. Effectiveness in selection would be specific to a particular environment. The selection for cultivar resistant to preharvest sprouting based on these characters should be deferred until later generations when the plants had reached

high level of homozygosity. The selection for low α-amylase and low germination at harvest ripeness would give more reliable protection against preharvest sprouting damage.

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CHAPTER 1

INTRODUCTION

THE NATURE AND OCCURRENCES OF PREHARVEST SPROUTING

Preharvest sprouting in wheat (*Triticum aestivum* L.) is the germination of grains in the ear before harvest. This occurs when non-dormant wheat cultivars are grown in areas conducive to germination i.e. moist weather conditions during harvest; or rainfall in the summer during ripening periods. Mares (1984) gave a definition for preharvest sprouting damage as "changes in the chemical constituents of the wheat kernel which accompany germination and which have deleterious effects on the subsequent commercial utilization of the wheat".

The sprouting damage problem is not confined only to actual sprouting in the ear, but also to internal levels of α-amylase, which in some wheat cultivars can be exceptionally high even in the unsprouted grains. Examples are a white spring wheat cultivar "Gamut" (Gordon *et al.*,1979), a winter wheat cultivar "Professeur Marchal" (Stewart, 1984), and the British cultivar "Fenman" (Cornford and Black, 1985).

Gordon (1980) has discussed germinability, dormancy and grain development in wheat at length. He pointed out that different cultivars or the same cultivar ripened in different environments have different patterns of grain development, and that dormancy could be due to either embryo immaturity, embryo dormancy or the lack of germinative α-amylase.

Preharvest sprouting damage reduces grain yield; test weight (which is the bulk density of the grain, in pounds per bushel or kilograms per hectolitre); and flour quality (McEwan, 1959; Belderok, 1968; Derera *et al.*, 1976; Bhatt *et al.*, 1981; Meredith, 1983; Lorenz *et al.*, 1983). Stoy (1983) estimated yield losses to range from 10 %

to as high as 30 - 50 % in years with exceptional damage. The reduction of flour quality results from increase in the activity of hydrolytic enzymes, particularly α-amylase (Perten, 1964; Bhatt *et al.*, 1981). High α-amylase levels result in starch breakdown during dough development and in early stages of baking giving "sticky" loaves with an irregular crumb structure (Buchanan and Nicholas, 1980; Evers and Stevens, 1985; Austin *et al.*, 1986). Mares (1984,1987b) emphasized that even a small number of sprouted grains can irreversibly damage an otherwise high quality sample.

To determine the α-amylase in the flour, a viscometric method known as the "Falling Number" test has been developed by Hagberg (1960) and Perten (1964). This method primarily measures the change in viscosity of a heated suspension of ground wheat due to enzymatic degradation of starch by α-amylase (Mathewson and Pomeranz, 1978). Bakery-type wheat flour normally has a Falling Number between 200 and 250, when the Falling Number lies below 150, there is great danger that the bread crumb will be sticky (Perten, 1964).

The problem of preharvest sprouting is found in every continent. One of the early reports of sprouting damage in wheat was in the United Kingdom (Greer and Hutchinson, 1945). Mac Key (1976) gave an extensive list of areas affected by preharvest sprouting. Included in the list were north Western Europe, the valleys of the Alpine region, western parts of Central Europe, south Chile, some regions of Argentina, Brazil north of 24° latitude, Kenya, the United States, Australia and New Zealand.

Climatic conditions conducive to sprouting can occur in any of the wheat-growing districts of New Zealand, but in some localities, such as Manawatu, the southern part of the Canterbury Plains, and Southland, sprouting damage occurs frequently (McEwan, 1967).

In western Canada, windrowing prior to combine threshing has become a predominant harvesting technique. Clark *et al.* (1984) reported that windrowing of wheat can lead to increased weathering

damage, particularly in susceptible cultivars. In 1968, Canadian wheat exported to Japan showed elevated levels of α-amylase activity (Czarnecki, 1987).

In the United States preharvest-sprouting of wheat is not a serious problem in the Great Plains because of favourable climatic conditions and modern rapid harvest techniques (McCrate *et al.*, 1981). The area affected by sprouting damage is in the Pacific North West States, (Washington, Oregon, and Idaho), and in the Eastern States, (Michigan in particular and New York) (Briggle, 1980). Sprouting damage in the Pacific Northwest may be caused by rain and the use of overhead sprinklers (Ciha and Goldstein, 1983). Cultivar differences between regions may also be one factor determining the occurrence of the problem. The Great Plains area produces the hard red wheat class which is suitable for making bread, whereas the Pacific Northwest is the principal production area of the soft white wheat class which is suitable for making pastry (Hehn and Barmore, 1965).

Wielenmann (1980) reported that in Switzerland over 42 per cent of the total wheat crop was destroyed in 1976 by preharvest sprouting. Sprouting damage, resulting in high enzymatic activity, was considered to be the most important problem in cereals in Sweden (Olered, 1963).

Australia is a country where white grain wheats are produced traditionally. The cultivars used are normally susceptible to preharvest sprouting. Mares (1987a) reported that in Queensland sprouting damage affects 15-20 % of the wheat harvest annually. Preharvest sprouting is considered a perennial problem in the wheat-belts of northern New South Wales and Queensland (Mares, 1984).

Recently, occurrences of preharvest sprouting in wheat in Asia have been reported. Fukunaka *et al.*(1987) reported that several wheat cultivars grown in Japan were susceptible to preharvest sprouting. In China, these problems were found in the southern winter wheat regions and north-eastern spring wheat region where the wheat crop matured during a rainy period (Wu, 1987).

Preharvest sprouting is closely associated with grain germinability, dormancy and enzyme activities in the grain at maturity (as will be discussed in Chapter 2, Review of Literature). The reports on the nature of gene effects of these traits were scarce. Accordingly, this present study was carried out to investigate the gene effects for grain growth, maturity, dormancy and α-amylase activity in three wheat crosses ripened in two environments. It complements the earlier work done by Gordon (1975) and Cross (1977).

CHAPTER 2

REVIEW OF LITERATURE

I) THE NATURE OF SEED DORMANCY

It has been generally accepted that seed dormancy is the dominant cause of resistance to preharvest sprouting in cereals. This first section of the review will give some details on the nature and types of seed dormancy.

Seed dormancy or primary dormancy has been defined as a state in which viable seed fail to germinate under conditions of moisture, temperature and oxygen favourable for vegetative growth (e.g. Amen, 1968). Villiers (1972) distinguished dormancy from quiescence in that dormancy is the state of arrested development whereby the organ or organism, by virtue of its structure or chemical composition, may possess one or more mechanisms preventing its own germination, but quiescence is a state of arrested development maintained solely by unfavorable environmental conditions such as inadequate water supply.

Another type of dormancy is called secondary dormancy or induced dormancy. In this kind of dormancy, the seeds are not initially dormant, but become dormant if exposed to conditions which are unsuitable for germination. An example of this kind of dormancy is wheat after exposure to high temperature (George, 1967). The term relative dormancy is either used to describe the situation where germinability is retained at lower temperatures and dormancy is manifested at higher temperatures (Vegis, 1964; Bewley and Black, 1982) or applied to a population of grains in a germination test when germination of viable seed is incomplete (P. Coolbear, personal comunication).

Bewley and Black (1982) divided primary dormancy into two types according to the causes (i) Embryo dormancy, where the control of dormancy resides within the embryo itself and (ii) coat-imposed

dormancy, in which dormancy is maintained by the structures enclosing the embryo, i.e. the seed coat. Pickett (1989) added the third type of dormancy to the classification by Bewley and Black (1982) as (iii) dormancy caused by germination inhibitors in the spikelet structures.

II) DORMANCY OF WHEAT GRAIN

Wheat grains are usually showed relative dormancy for a short while after harvest, and at that stage will not germinate at 20°C. If however the temperature is lowered to 15°C, nearly all the grains germinate. After the loss of dormancy, germination occurs at both temperatures (Bewley and Black, 1982; Bryant, 1985). There are many exceptions from the previous statement, the obvious one being when preharvest sprouting of wheat or cereal at maturity occurs because the grain are not dormant at maturity. When the weather is wet during harvest times, these grains will germinate in the ears. The dormancy which is relevant to the preharvest sprouting problem is the primary dormancy rather than secondary dormancy.

The causes of dormancy in the wheat grain has long been studied, but the information obtained has rarely been put together to obtain a conclusive answer. This review will only bring in some relevant information involving wheat grain dormancy. The review will separate into 3 sub-topics: (i) structure of the wheat grains (ii) the role of grain coat and (iii) hormonal effects.

II.1) Structure of the Wheat Grain

A wheat grain is a caryopsis, a dry one-seed fruit. The pericarp (fruit coat) envelops the seed and is fused with the thin seed coat (testa). Together they form two protective layers around the endosperm and the embryo (Bradbury *et al.*, 1956a). The pericarp and the outermost tissues of the seed itself, including the aleurone layer, comprise the bran. There was variation in the components of bran. Meredith (1967) considered that bran did not include aleurone layer. The difference in component of the bran arises from the

variation in percentage of the flour recovered from milling process. Dewdney and Meredith (1979) stated that "In countries where the extraction rate of flour from wheat grains is below 72 % the aleurone is not included in the flour".

From the outside inward, the pericarp of wheat is composed of epidermis, hypodermis, thin-walled cells, intermediate cells,cross cells, and tube cells. The seed coat (testa) is located between the pericarp and the nucellar epidermis and is firmly joined to either tube cells or cross cells on the outside and to the nucellar epidermis on the inside. The seed coat may be separated into 3 layers: a thick outer cuticle, a "colour layer" that contains pigment, and a very thin inner cuticle (Bradbury *et al.*, 1956b). This cuticular layer inside the testa is derived from the nucellus (Cochrane and Duffus, 1979).

The endosperm contains the aleurone layer which is an unicellular layer in wheat (Phillips and Paleg, 1972), and the starchy endosperm which is non-living tissue in the quiescent cereal caryopsis, containing carbohydrate and protein reserves (King, 1989). The embryo is located in the dorsal side at the base of the caryopsis and comprises the scutellum, and embryonic axis. The embryonic axis comprised of shoot meristem covered by the coleoptile and root meristem covered by the coleorhiza. Between the endosperm and embryo there is a layer of epithelial cells. The empty endosperm cells close to the epithelial layer formed the "crushed layer" (Percival, 1921). Scutellum is the rudimentary cotyledon in the embryo.

The pericarp is diploid tissue which has the same genetic constitution as the maternal plant. Endosperm is triploid developed from the primary endosperm nucleus, which is formed by the fusion of two haploid polar nuclei and the second haploid nucleus of a male gamete. The embryo is diploid derived from the fusion of a haploid ovum and a haploid pollen nucleus. Diagram of the wheat grain structure is presented in Figure 1.

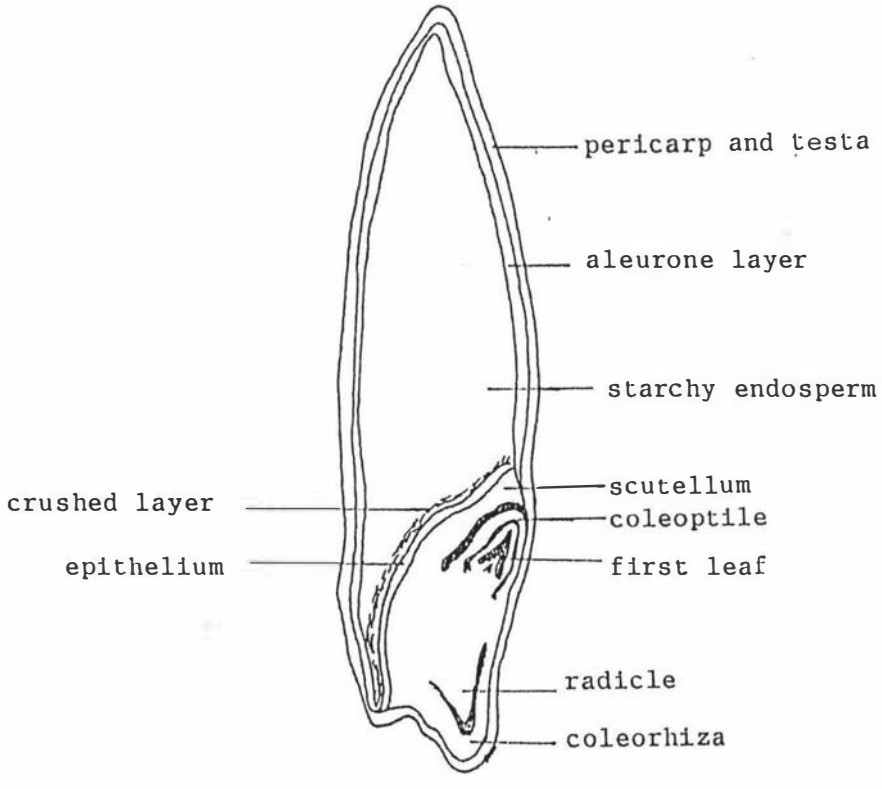

Figure 1. Diagram showing the structure of the wheat grain (modified from Bewley and Black, 1978).

II.2) Role of Grain Coat

The grain coat has been considered as a cause of dormancy in wheat in one of the following ways; (i) by preventing the uptake of water (ii) by preventing the gaseous exchanges (oxygen or carbon dioxide) (iii) inhibiting germination by inhibitors in the coat (iv) imposing a mechanical restraint to the embryo. Each of these hypotheses has been tested with different results.

Wheat grains will often germinate if the pericarp is removed (Belderok, 1961). Radley (1979) reported that the isolated embryos of winter wheat cv. Cappelle Desprez germinated readily from 3.5 weeks after anthesis, where as the intact grains did not germinate until nearly 7 weeks after anthesis. Removal of the outer pericarp permitted the grain to germinate at a young age like the isolated

embryo. Wellington (1956b) observed that the effect of the covering layers did not appear to be related to their permeability to water or oxygen. Instead, dormancy was caused by the mechanical strength of the covering layers (Wellington, 1956b; Wellington and Durham, 1961). In contrast, Miyamoto *et al.* (1961) concluded from germination tests of excised wheat embryo which had adhering seed coat layers that the mechanical strength of the seed coat was not the cause of grain dormancy neither was dormancy caused by restricted water or oxygen uptake. Previously, Miyamoto and Everson (1958) carried out an analysis of the pigment in the wheat grains. Several varieties of wheat were grown either in the field or in the greenhouse and were harvested at the dough stage. The grain coverings were then separated into two fractions, the pericarp and the seed coat with a portion of aleurone layer adhering. They found a close positive correlation between the degree of grain redness and the quantity of catechin and catechin tannin present. The amount of catechin and catechin tannin was found mainly in the seed coat while the pericarp contains only a trace amount. Miyamoto and Everson (1958) postulated that post harvest dormancy in wheat might be caused by an inhibitor which could be catechin, catechin tannin or their precusors.

Catechin tannins (or condensed tannins) are formed by the condensation of hydroxyflavans i.e. catechins (flavan-3-ols) or leucoanthocyanidin (flavan-3,4-diols) (Ribéreau-Gayon, 1972). These phenolic compounds are precusors of the red pigment phlobaphene. Polymerization of cathechin tannin to phlobaphene involves the enzyme complex polyphenol oxidase (Taneja and Sachar, 1974; Taneja *et al.*, 1974).

Gordon (1975) conducted an experiment to test the effect of flavan-3-ols in inhibiting the germination of the wheat grain *in vivo*. One and a half year old seeds of two white-grained (Gamut and Timgalen) and 2 red-grained genotypes (Sonora 64A and Pembina) were used. Grains were imbibed in six concentrations of cathechin solutions (0, 10, 50, 100, 250 and 500 $\mu g. ml^{-1}$). The result showed that concentration of catechin solutions had no effect on the level of

flavan-3-ol in the grains after 24 hours imbibition. The variation of flavan-3-ol among genotypes was due to the endogeneous level prior to imbibition. The result of germination test of the grains after 72 hours imbibition was analysed by Freedman's rank Chi-square. The result indicated that there were no significant differences among the genotypes or among the solution concentrations in germination fraction. Furthermore the correlations between flavan-3-ol levels in the imbibed grains and germination fraction were +0.622 (**) and +0.981 (*) for phenotype and genotype respectively. The positive correlations obliterated the hypothesis that flavan-3-ols inhibited germination.

Stoy and Sundin (1976) tested the inhibitory effect of catechin tannins on the germination of isolated wheat embryos. They found that 0.3 % catechin tannin inhibited the germination of wheat embryos, and the inhibitory effect of catechin tannin was eliminated if 10^{-6} M GA_3 was added into the agar. Gordon (1979) investigated the level of flavanols (flavan-3-ols and flavan-3,4-diols) in four wheat cultivars with different grain coat colour and different levels of dormancy. He reported no difference in level of flavanols in the four genotypes and concluded that flavanols did not inhibit germination *in vivo*. He proposed two hypotheses linking embryo dormancy with grain redness:

(i) the polyphenol oxidase complex, which polymerizes flavanols to the putative pigment phlobaphene, contributes towards embryo dormancy by induction of hypo-oxia, or

(ii) that the pigment itself and it tannin complexes cause hypo-oxia.

Belderok (1961) reported that disulfide and thio groups in the cell walls of the outer layers of the caryopsis were correlated with dormancy. Paulsen and Heyne (1983) reported the existence of inhibitor extracted from pericarp of wheat grain. The inhibitor has an inhibiting effect on the germinability of excised embryos. The inhibitor has been characterized as a phenolic derivative, soluble in water, present in both red and white grain wheat genotypes and did not diminish during after-ripening. Recently Morris and Paulsen (1988)

found that the bran fraction of the milled white wheat grain contained a germination inhibitor. The inhibitor was soluble in water and up to 90 % ethanol, insoluble in petroleum ether, and heat stable.

It has been observed that cultivars with red grain were more dormant than cultivars with white grain (Hutchinson *et al.*, 1948; Wellington and Durham, 1958; Gfeller and Svejda, 1960; Everson and Hart, 1961). However a discrepancy from this relationship have been reported. For example Derera *et al.* (1977) have identified white seed coat wheats possessing a relatively high degree of dormancy e.g. Kenya 321 sib and Ford. Some red grain cultivars has little or no dormancy e.g. Sonora 64A (Gordon, 1979). Reitan (1980) found that intensity of grain coat colour was poorly correlated with seed dormancy ($r = 0.387$). Also Gordon (1983b) reported a moderate negative correlation between grain redness and sprouting as judged by grain appearance. Some white-grained wheats have shown to be sprouting resistant (Gordon, 1983a).

Huang *et al.* (1983) studied the caryopsis structure of 14 cultivars of wheat by scanning electron microscopy. they reported that white wheat cultivars exhibited looser integument structure and greater separation between the seed coat and tube cells of the inner pericarp than did red wheat cultivars. The pericarp of white wheat was frequently folded and generally weaker than that of red wheats. Water was imbibed faster and penetrated deeper into the kernel of the white wheats than into the kernels of the red wheats. Wellington (1956) observed that the delay in germination of the red grains was due to constraint imposed by the intact epidermis being greater than in the white grains. Also Belderok (1976) reported that the testa of a sprouting resistance wheat maintained its integrity beyond grain maturity whereas the structure of testa in susceptible cultivars became granular before maturity. All the observations related to the mechanical barriers imposed by grain coat lend support to the proposed hypotheses of hypo-oxia which might inhibit germination (Gordon, 1979b; 1980).

II.3) Hormonal Effect on Grain Dormancy

It has been suggested that seed dormancy may involve an interplay between endogenous growth inhibiting and growth promoting substances (Amen, 1968; Villiers, 1972; Villiers and Wareing, 1965; Khan, 1975; Mayer and Poljakoff-Mayber, 1982).

II.3.1) Gibberellic Acid (GA)

The gibberellins are generally recognized as regulators of growth and development of higher plants (Hedden *et al.*, 1978). The pathway leading to the formation of GAs comprises three steps: (1) mevalonic acid to kaurene, (2) kaurene to GA_{12}-aldehyde and (3) GA_{12}-aldehyde to GAs (Khan, 1982).

Mounla and Michael (1973) measured the amount of "bound" GAs and "free" GAs in two varieties of barley. They reported that "bound" GA activity fell to a low level on the 9^{th} day after pollination, and increased towards a maximum on the 32^{nd} day, after that it decreased again up to maturity. Slominski *et al.* (1979) also obtained a similar result with barley, they found that the peak of GA_3 concentration occured at milk ripeness (about 20 days after anthesis). In wheat, the gibbellin content of grains increased until 3 weeks after anthesis then decreased (Wheeler, 1972). Mounla and Michael (1973) postulated that before the 32^{nd} day after pollination, part of the "free" GAs was converted to "bound" GAs. Their results showed that after 12^{th} days from pollination the curves for the rate of dry weight increase and for "free" GA-content run more or less parallel to each other but the GA content reaches its maximum 2-4 days earlier than that of the dry weight. They proposed that GA may affect the assimilation of dry weight in the grain. Radley (1976) reported a sharp increase in GA at the time when wheat grains reach its maximum volume but the dry weight is still low.

Even though a build-up of active GA might be essential for seed development and growth, other factors, including other promotors and inhibitors might modify GA control of seed growth (Khan, 1982).

Gibberellic acid at the concentration as low as 200 ppm up to 0.1 % can replace the low temperature treatment in dormancy breaking in wheat (Belkendam and Bruinsma, 1965; Kahre, *et al.*, 1965). In wheat, Radley (1976) found no correlation between the content of free GA and the germinability of either isolated embryos or intact grains at various time after anthesis. However the bound growth substances released by enzyme action showed some correlation with germination. Exogenous application of gibberellic acid (10 $\mu g\ ml^{-1}$) to the intact grain stimulated germination during the later stages of development (Radley, 1979). Gosling *et al.* (1981) showed that exogenous application of GA_3 at 13°C stimulated both the rate and maximum percentage germination of young wheat grains but the effects became less pronounced as grain development proceeded.

Gibberellin regulates the synthesis of α-amylase in germinating wheat grain (Rowsell and Goad, 1964) and in barley (Varner, 1964; Varner and Chandra, 1964; Filner and Varner, 1967; Jacobsen and Varner, 1967). Groat and Briggs (1969) investigated the formation of α-amylase in germinating barley and observed the time lag between the appearance of gibberellin in the endosperm and the appearance of α-amylase. They concluded that gibberellin originated from embryo was important in regulating the synthesis of α-amylase in the aleurone layer in malting grain.

Evins and Varner (1971) reported that gibberellic acid increase the rate of synthesis of the endoplasmic reticulum in barley aleurone cells. They suggested that the increase in endoplasmic reticulum synthesis precedes and is probably required for the GA-induced synthesis and release of hydrolytic enzymes. Baulcombe and Buffard (1983), using hybridization and *in vitro* translation techniques, demonstrated that GA_3 influenced the actual level of α-amylase mRNA, thus one control point for the hormone is at the transcriptional level. More recently, this has been confirmed in more detail in the barley system by Deikman and Jones (1986).

Trewavas and Cleland (1983) have discussed the important of plant hormones in regulating the developmental processes in plant. They have an opinion that sensitivity of tissues to plant hormones (plant growth substances) has an important role in determining the developmental processes. Trewavas contended that only the tissues sensitivity alone determined the developmental processes, while Cleland thought that both the concentration of the hormones and the sensitivity of the tissues were important. The results of experiment by Walker-Simmons (1987) and by Wiedenhoeft *et al.* (1988) in wheat supported this hypothesis (see section II.3.2 this chapter). Paulsen and Heyne (1983) have reported that the ability of the embryos to respond to the endogenous inhibitor was high in fresh seeds and decreased during after-ripening. They observed that embryo of sprouting resistant genotypes have strong response to endogenous inhibitor. The inhibitor was not identified but was characterized (see also II.2 this chapter).

In wheat, the insensitivity to GA in some cultivars has been reported. Gale and Marshall (1973) found that dwarf wheat cultivars "Minister Dwarf" and "Tom Thumb" are insensitive to GA and thus do not produce α-amylase in response to the hormone. Gale and Marshall (1975) have shown by an embryo transplantation technique that the lack of response was a function of endosperm tissue and that GA release from the embryos of insensitive genotypes during germination was similar to that of sensitive genotypes.

Both Radley (1970) and Gale and Marshall (1975) reported that GA-insensitivity in the Norin type dwarfs manifested its effect only in the shoot, but the aleurone or endosperm of these cultivars respond to GA in a similar manner to the seeds of tall wheats. The GA insensitivity in the aleurone appeared to be controlled by different genes from the GA insensitivity in the shoot, or in the coleoptile (see also section VII.2, this chapter).

Ho *et al.* (1981) studied the effect of GA in two wheat cultivars: D6899, a GA insensitive dwarf wheat, and Nainari 60, a standard height cultivar. They found that both cultivars have the

same uptake and metabolism of gibberellin, and the abscisic acid levels in both cultivars are not much different. King *et al.* (1983) obtained similar results when they compared dwarf and tall wheats for abscisic acid levels in either turgid or partially dehydrated leaves. They found no differences in ABA level between the two types of wheat, which implied that ABA was not involved in any GA insensitivity mechanism.

The aleurone tissue of immature wheat grains is usually non-responsive to gibberellin, with respect to α-amylase production. In the immature grains the responsiveness can be induced by drying (Nicholls, 1979; King and Gale, 1980; Armstrong *et al.*, 1982). Enhanced sensitivity resulting from drying is not caused by a change in gibberellic acid uptake. A possible mechanism for the change in the sensitivity of aleurone cells might be through structural alterations in cell membranes (Armstrong *et al.*, 1982).

Nicholls (1986a) has shown that dehydration is not necessary and that detachment alone is sufficient for the development of GA_3 sensitivity. In the later experiments (Nicholls, 1986b), the wheat ears were cultured on a medium containing sugar. In this condition the loss of water from the ears was very little. The results showed that GA_3 sensitivity in the aleurone of grains from cultured ears was comparable to the sensitivity of aleurone of grains from the dried ears.

King (1976) reported the effect of premature drying of wheat grains on germinability. As early as 10 days after anthesis and at anytime thereafter grain germination and amylase induction were possible if the grain was air-dried in the ear for only 1 week. He concluded that grain drying may actually enhance ABA breakdown.

Detaching wheat grains from the ear and maintaining them under conditions of high humidity for an equivalent time to the drying treatment occasionally results in the induction of a GA-responsive

state. Also the embryo/scutellum from a developing wheat grain can produced α-amylase when the tissue is excised from the grain and incubated on agar (Cornford *et al.*, 1987).

Singh and Paleg (1984a) found that low temperature (5°C) significantly increases gibberellic acid sensitivity (measured as α-amylase production). This low temperature induction of GA_3 sensitivity was found to be operative in aleurone tissue of the dwarf varieties carrying at least one of the three Rht alleles. They postulated that the low temperature effect probably involved an increase in active hormone (GA_3) receptor sites. Singh and Paleg (1984b) further observed that low temperature also caused the changes in the content of the lipids, especially phospholipids. This result suggests that GA_3 receptor sites are membrane based as had been proposed by Wood and Paleg (1972, 1974). The contention that sensitivity to GA_3 involves membranes was supported by Armstrong *et al.* (1982).

Khan *et al.* (1973) studied the GA-induced enzyme formation in the embryoless grains of wheat cv. Yorkstar. Their results demonstrated that in the absence of GA_3 the embryoless grain is unable to synthesize α-amylase. Yorkstar wheat has a high percentage of embryoless grains (about 10-11 %). This phenomenon lead some scientists to think of the possibility to produce embryoless wheat for bread making purpose (Marshall, 1987). If the production of embryoless grains of wheat is attainable it would be a better approach to solving the sprouting problem compared to the proposed "RaiKai Process" whereby grains were cut so that embryo attached part could be grown and deembryonated part could be milled (Meredith, 1962; Meredith and Pomeranz, 1985).

Other hydrolytic enzymes which were produced by aleurone of germinating grain of barley when treated with GA_3 included protease (Jacobsen and Varner, 1967) and α-glucosidase (Hardie, 1975).

II.3.2) Abscisic Acid (ABA)

Addicott and Lyon (1969) have reviewed the role of abscisic acid (ABA) in plants as (a) acceleration of abscision in fruits and leaves; (b) induction and prolongation of dormancy in the shoot of dedicious trees and in tubers; (c) inhibition of germination by prolonging the dormancy of seeds; and (d) inhibition of flowering of long-day plants when held under short days.

Milborrow and Robinson (1973) have demonstrated that ABA can be synthesized from mevalonate in the embryos and endosperm of developing wheat grains. The increase in grain ABA levels during development could arise from *de novo* synthesis of ABA within the grain, or from transport of ABA synthesized elsewhere in the plant into the grain via the phloem, or from a combination of these processes (Jacobsen and Chandler, 1987). However, King (1979) has demonstrated that in detached, cultured ears of wheat the content of ABA still increased to the same extent as in the grain of ears on plants in the glasshouse.

Radley (1976) found that a strikingly high concentration of ABA occurred in the outer pericarp 3 weeks after anthesis but later most of the ABA was found in the endosperm and surrounding layers. The maximum peak of ABA in the wheat grain was reported to occur at about 40 days after anthesis (McWha, 1975; King, 1976; King, 1979). The peak of ABA level occurred at about one week before maximum dry weight (McWha, 1975) and it preceded the water loss from the grain (Radley, 1976). The bulk of ABA in an ear was in the grain (95 %) and the husk contained only 5 % of the total ABA. Within the grain , the embryo contributed 19 %, the testa and endosperm contributed 76 % (King, 1976). He also observed that full germinability was attained 40-60 days after anthesis in association with the loss of grain water and decrease in ABA. He suggested that the accumulation of ABA at the later stage of the grain growth prevented precocious germination and premature hydrolysis of starch reserves of the morphologically mature but still unripe grain. Koch *et al.* (1982) reported that exogenous application of ABA (1 µg/l) inhibited radicle growth of both sprouting

resistant and susceptible cultivars in the absence of pericarp tissue. But when a portion of pericarp was left attached to the embryo, the germination was inhibited only in resistant cultivars.

In barley, Higgins *et al.* (1982) reported that ABA reversed all the effects of GA_3 on protein synthesis and mRNA levels in the aleurone layers. This result was supported by Chandler *et al.* (1984). Mundy (1984) reported that ABA induced the α-amylase inhibitor in barley aleurone layers and suggested that the inhibitor functioned as an active mediator of amylase activity during the development and germination of barley seeds. Stoy and Sundin (1976) showed that germination of isolated wheat embryos was inhibited if 5×10^{-5} M of ABA was added. GA_3 at the level of 1×10^{-5} M suppressed the effect of ABA.

However, Verry (1978) reported that the concentration of ABA in developing wheat grains was not related to either dormancy or to maturation and dehydration of the grain. Radley (1979) also found no obvious relationship between changes in ABA and germinability of wheat grains. The results of an experiment by Walker-Simmons (1987) showed that embryonic ABA levels of a sprouting resistant wheat cultivar, Brevor, and a susceptible cultivar, Greer, are similar. The embryonic levels in the cultivar Greer average 75 % that of the sprouting resistant cultivar Brevor. However ABA inhibited embryonic germination more in the sprouting resistant cultivar than in the susceptible cultivar. Wiedenhoeft *et al.* (1988) compared endogenous levels of ABA in the embryo and rate of germination of embryos in two cultivars of wheat grown in the field in two different years. The embryonic ABA levels during grain development are within the range of the previous reports (cf. King, 1976; Radley, 1979; Walker-Simmons, 1987). Free embryonic ABA was influenced more by environment and stage of development than by cultivar. No consistent relationship between endogenous levels of ABA and embryonic germinability in water at any stage during embryonic development has been reported. But exogenously applied ABA reduced the rate of germination of dissected embryos, regardless of year, cultivar, or stage of development when

compared to germination in water. The resistant cultivar Brevor was inhibited more than the susceptible cultivar Greer. Wiedenhoeft *et al.* (1988) postulated that difference in embryonic sensitivity to ABA may contribute to cultivar differences in resistance to preharvest sprouting.

II.3.3) Cytokinins

Cytokinins are ubiquitous in plants either as free substances or as structural components of t-RNA, their effect has been postulated to trigger mitosis (Hall, 1973). A transient peak of biologically active cytokinins has been detected in developing wheat grains during the first six days after fertilization (Wheeler, 1972; Durley and Morris, 1983). In wheat grain, cytokinins were localized largely in the endosperm and cytokinin was higher in normal grains compared with the naturally embryoless seeds suggesting that the presence of an embryo is essential for synthesis or accumulation of this hormone (Thomas *et al.*, 1978). Exudates from young stems contained cytokinins and this may originate in the roots and move to the ears through the stems (Wheeler, 1972).

Eastwood *et al.* (1969) reported that the endosperm of wheat contain a compound which has cytokinin activity and which was responsible for the induction of essential metabolic processes in the aleurone cells of the germinating wheat grain. The mechanisms of action of cytokinin in germination is not known. Applied cytokinins usually display low activity in dormancy and germination control compared either to ABA or GA. Their activities are prominent when combined with other promotive agents such as GA, light, and ethylene (Taylorson and Hendricks, 1977). The role of cytokinins could be to control the movement of gibberellins and other plant chemicals within and from the embryo thus triggering other biochemical processes leading to germination (Thomas, 1977).

III) PREHARVEST SPROUTING IN WHEAT

It was generally accepted that seed dormancy was the dominant cause of preharvest sprouting resistance in cereals (Harrington, 1949; Belderok, 1968). However, there are many other factors which may contribute to preharvest sprouting resistance. Derera *et al.* (1977) reported the presence of germination inhibitors in the bracts of the wheat cultivar Kleiber. King (1984) found that 18 % of the varietal differences in sprouting can be accounted for by differences in ear and grain water uptake. King and Richards (1984) have shown that wheat lines with awns absorbed more water and showed greater sprouting in the ear compared with the awnless near-isogenic lines. Furthermore they found that the "club-head" character enhanced ear water uptake whereas pubescence and glaucousness had no effect on ear wetting. They suggested that selection for awnless lines will contribute to sprouting resistance to some extent.

Endosperm insensitivity to gibberellins in wheat has been reported to be a factor contributing to sprouting resistance (Gale and Marshall, 1973; Gale, 1976; Derera *et al.*, 1976; McMaster, 1976). This characteristic will be discussed later in section VII.2.

Numerous characters have been used as indicators of preharvest sprouting resistance. Some characters are direct measurements of the sprouting propensity, *e.g.* radicle elongation, while others are related to endosperm degradation or levels of enzyme activity.

Different types of germination test have been used to measure preharvest sprouting resistance e.g. germination testing of threshed seeds or intact spikes in wet sand (Harrington and Knowles, 1940; Everson and Hart, 1961; McEwan, 1976); artificially wetting the intact spikes (Hutchinson *et al.*, 1948; McMaster and Derera, 1976; Gordon *et al.*, 1977). Hagemann and Ciha (1984) compared germination tests with intact spikes and threshed seeds at different temperatures. Their comparison was based on three winter wheat cultivars varying in susceptibility to preharvest sprouting which were grown in six

different environments. The methods which were considered as effective had to show significant differences in both cultivar and environment effect at a given germination temperature. They concluded that a germination test using intact spikes rolled in paper towels and the test using threshed seeds in Petri dishes at 20°C were effective methods in differentiating dormant cultivars from non-dormant cultivars.

Gosling *et al.* (1981) contended that assessment of germination at a time less than 15 days(d) from the beginning of the test would not reveal the full germination potential of grains but only reflect the rate of germination. They suggested that data on germination rate alone could not be reliably interpreted in terms of seed dormancy. However, during the course of germination, the ranks of germinability of the grains with different ages did not change. This implied that a shorter incubation time for germination, such as 5 days or 7 days may be enough to measure the germinability. Also Gordon (1975) has suggested that serial samplings during grain maturation can be substituted for an extended test, enabling the *in situ* changes in the embryo maturity and dormancy to be followed directly. He observed that after the first three days of a test no change in germination occurred. Other difficulties that may arise when the grain are incubated for a long period are the contamination by saprophytic fungi, and the need for more facilities when dealing with a larger number of samples.

The technique of placing wheat spikes in a rain simulator has also been used (McMaster and Derera, 1976; Gordon *et al.*, 1977; Czarnecki, 1987). McMaster and Derera (1976) suggested that in screening for resistant lines sampling of the ears should be done at 5 ,15 and 25 days after harvest ripeness (12-14 % grain moisture) to provide adequate protection from preharvest sprouting damage. With this system, Derera *et al.* (1976) reported significant correlations between the α-amylase activity after 48 hour wetting with the sprouting damage scores, in 12 wheat cultivars. The same result was obtained in the F_2 lines derived from a cross between "Tordo" and Tr 450-16 (Bhatt *et al.*, 1976).

Other characters which have been used for selection against preharvest sprouting are α-amylase activity (Bingham and Whitemore, 1966; ; Moss *et al.*, 1972; McMaster and Derera, 1976; McEwan, 1980; Meredith, 1982) and Falling Number (Olered, 1963; Tedin and Persson, 1963; Moss *et al.*, 1972; Svensson, 1976 ; Weilenmann, 1976). Comparing the Falling Number test and direct assay for amylase led Gordon (1978) to suggest that the falling number measured all aspects of endosperm degradation, including amylase effects.

Gordon *el al.* (1977) measured the level of α-amylase in one year old seeds of Timgalen wheat. They observed that increased in α-amylase activity started at about 36 hours after grain imbibition and the sprouting preceded increased α-amylase activity by at least 20 hours.

While germination tests are better in predicting sprouting itself (embryo elongation) the enzymatic test measures the actual endosperm damage due to sprouting (Gordon, 1978; Hagemann and Ciha, 1984). McCrate *et al.* (1981) studied the effects of simulated rain on hard red winter wheats and hard white winter wheat. The wheat cultivars were grown in the field, and harvested when the grain was harvest ripe (<16 % moisture). Sprout-inducing treatments were no rain and rain at 0, 2, and 4 weeks after harvest. They reported that sprouting and α-amylase activity were positively and highly correlated. However the effects of simulated rain on α-amylase activity and Falling Number were modified greatly by the date of treatment and by cultivar. They suggested that low visual sprouting and low α-amylase activity are not mutually inclusive, so both characters should be selected for. Henry and McLean (1987) tested the sprouting of intact heads of three varieties of wheat under controlled conditions. They found significant correlation between α-amylase and visual sprouting (r = 0.83). But the relationship between α-amylase and sprouting was dependent upon the wheat variety as well as the temperature.

Perten (1964) reported that the relationship between the Falling Number and the α-amylase activity in wheat and rye are curvilinear. However the liquefaction number is linearly related to α-amylase activity , where liquefaction number is derived as follows: Liquefaction number = 6,000 / (Falling Number - 50). Mathewson and Pomeranz (1978) studied the relationship between alpha amylase and Falling Number in wheat. Their results showed that Falling Number values for the sprouted white wheats were higher than those for the hard red winter wheats at the same level of α-amylase. Ringlund (1980) reported differences in Falling Number at a given level of α-amylase activity in spring wheat harvested at different maturity stages. He also found that varieties with high dormancy normally have a high falling number. Moss (1987) stated that the relationship between α-amylase and Falling Number was affected by many factors which combine to introduce considerable errors in predicting one from the other. His results supported the finding of Ringlund (1980) that cultivars vary in their falling numbers, even at the same α-amylase level.

Breeding white wheat for resistance to sprouting damage has been an objective of wheat improvement programs in a few countries. Mares (1987) has screened a number of white wheats for new sources of sprouting tolerance. Among recent Australian varieties released which showed resistance to sprouting were Seneca and Sunelg. These two varieties combined resistance to sprouting from one parent with high yielding, disease resistance and good quality from other parent. He stated that low Falling Numbers in apparently sound, mature grains do not necessarily preclude the use of such varieties in a variety improvement program. As an example, Seneca is derived from Spica which normally has a low falling number (200 sec) and a high α-amylase activity at maturity. He commented that the factors which control grain germinability and sprouting in the ear can be separated from those which condition low falling number and high α-amylase activity in the mature grains of particular varieties in the absence of sprouting. De Pauw and McCraig (1987) assessed different techniques to identify sprouting resistant lines from hybrid

populations derived from crosses between five parental genotypes with 0-3 genes for red kernel colour. They found that neither measure of α-amylase activity determined by gel diffusion or by Hagberg Falling Number techniques based on non-weathered samples from the field were related to the variables used to measure sprouting resistance and α-amylase activity on samples subjected to simulated rain. Visible evidence of sprouting in intact spikes related quite well to the percentage of germinated kernels and α-amylase activity. They recommended that using evidence of visible sprouting on a samples of 10 spikes per lines, permits a rapid and effective separation of a population into sprouting susceptible and sprouting resistant categories. Recently, Upadhyay and Paulsen (1988) evaluated F_2 and F_3 lines from six crosses which had Clark's Cream, a white grained sprouting resistant cultivar, as the male parent. They reported that the extent of sprouting in simulated rain had a negative correlation with Falling Number in five crosses and positive correlation with α-amylase activity in four crosses. However, because the correlation values are low, they suggested that Falling Number and α-amylase activity are not appropriate selection criteria. They supported the recommendation made by Gordon (1983) and by De Pauw and McCaig (1987) that screening of lines for sprouting resistance should be based directly on sprouting attributes themselves.

IV) EFFECTS OF TEMPERATURE ON GRAIN DEVELOPMENT AND PREHARVEST SPROUTING

IV.1) Effects on Grain Development

Wardlaw (1970) reported a reduction in the individual grain weight of wheat cultivar Gabo when it received low temperature (15°C/10°C) treatment during 15-25 days from anthesis compared with 21°C/16°C and 27°C/22°C treatment. There was interaction between light intensity and temperature in such a way that the reduction in grain weight due to low light, was greatest at high temperature. Sofield *et al.* (1977) and Spiertz (1977) reported that the duration of grain growth decreased as temperature rose. Also they reported that an increase in temperature increased the rate of growth per grain. This was supported by Donovan *et al.* (1983). Warrington *et al.* (1977) found that wheat plants grown at low temperature during ear development had more potentially fertile florets in each spikelet and that low temperature during grain filling period (20°C and 15°C) resulted in heavier individual grains compared to high temperature (25°C).

Campbell and Davidson (1979) found that seed set of primary and secondary florets and seed weight of Manitou wheat were inversely related to temperature.

IV.2) Effects on Grain Dormancy and Preharvest sprouting

Belderok (1961) reported that high temperature during the transition from milk- to mealy-ripeness affected duration of dormancy of wheat grains. The high temperature during this period reduced the average duration of the dormancy. Also Belderok (1968) reported that hot weather during the dough stage of grain development shorten the dormancy period, while cool weather extended it. Nielson *et al.* (1984) studied the effect of weather variables during maturation on preharvest sprouting of winter wheat, they reported that sprouting was increased by large daily temperature fluctuations, low daily

temperatures and high precipitation. Reddy *et al.* (1985) observed that high temperature during the grain filling period (26°C) induced lower dormancy levels whereas the low temperature (15°C) induced higher levels of dormancy. The degree of expression of the dormancy level depends on the temperature at which the seeds are germinated. A low germination temperature (15°C) is effective for breaking dormancy and thus less dormancy is expressed. Strand (1989) also reported the effect of high temperature and high radiation during preharvest generally reduced seed dormancy.

Synchrony of maturation traits such as embryo maturity, embryo dormancy, base α-amylase and germinative α-amylase with harvest ripeness in wheat was reported to be affected by genotype and temperature regime during the grain development period (Cross, 1977; Gordon, 1978). Gordon (1978) found that lack of germination in the cool environment was due to embryo immaturity rather than dormancy, and this happened to all the four genotypes of wheat studied.

Plett and Larter (1986) experimented with one wheat line, RL4137 and three triticale lines and reported that there existed an interaction between germination temperature and maturation temperature. They concluded that germination tests at 25°C produced tolerance ratings that consistently differentiated among genotypes over a range of stages of kernel development as well as different temperatures during kernel maturation. But the germination data for RL4137 wheat showed that the effect of maturation temperature manifested itself clearly when grain were germinated at 17°C. For this wheat line the higher the maturation temperature the lower the sprouting score.

V) α-AMYLASE

Defined as an endo, α-1,4-glucan 4 glucanohydrolase (E.C.3.2.1.1) (Meredith and Jenkins, 1973), α-amylase is a group of enzymes which has an important role in the breakdown of cereal endosperm. Three types of α-amylase in cereal grains have been

reported so far. The first group, α-amylase 2, has been referred to as green α-amylase (Olered and Jönsson, 1970), group II (Sargeant, 1979, 1980), GI and GII (Marchylo *et al.*, 1980) and called I by Daussant *et al.* (1980). Characteristics of α-amylase 2 are that it has a broader pH optimum, greater heat labilities, and a higher molecular weight compared to the second group of α-amylases (Marchylo *et al.*, 1976). The isoelectric points of α-amylase 2 ranges between 4.5-5.1 (Marchylo *et al.*, 1976; Sargeant,1980). The second group of α-amylases, α-amylase 1, is a major constituent of α-amylase in germinated seeds. This group of α-amylase was known by other names as II or malt (Daussant *et al.*, 1980), group I (Sargeant, 1980) and G III (Marchylo *et al.*, 1980). α-amylase 1 has an isoelectric point around 6.0-6.5 (Tkachuck and Kruger, 1974; Sargeant, 1980) and the pH optimum for enzyme activity is between 5.5-5.6 (Tkachuck and Kruger, 1974). It is only α-amylase 1 that is able to absorb onto and subsequently degrade the undamaged raw starch granule (Sargeant, 1980). Adsorption of α-amylase to the starch granule is a prerequisite for starch degradation.

Daussant *et al.* (1979) reported that there was a third group of α-amylase in wheat which they called III (here referred to as α-amylase 3). This group of enzymes are found in developing seeds only, and differs from α-amylase 2 and α-amylase 1 in that it shows cathodic migration, when electrophoresed at basic pH (α-amylase 1 and α-amylase 2 migrating towards the anode under these conditions). Daussant and Renard (1987) found that this third group of α-amylase has an isoelectric point above 10.

There are reports that immature kernels of wheat contain high levels of α-amylase and the level falls rapidly as the grains mature (Olered and Jönsson, 1970; Kruger, 1972a; Meredith and Jenkins, 1973; Dedio *et al.*, 1975; Marchylo *et al.*, 1976; Daussant *et al.*, 1979; Marchylo *et al.*, 1981; Daussant and Renard, 1987). The α-amylase level in wheat kernels during development reached a maximum level about 10-15 days after anthesis (Dedio *et al.*, 1975). The enzyme in the immature grains is found largely in the pericarp (Kruger, 1972a;

Meredith and Jenkins, 1973; Dedio *et al.*, 1975). Since the pericarp of immature wheat grains contain massive amounts of small starch granules, it was postulated that the amylase activity in the grain at this stage was associated with metabolism of the pericarp starch (Meredith and Jenkins, 1973). Daussant and Renard (1987) reported in the pericarp of developing wheat kernel, α-amylase 2 and 3 are both present. The low pI form (α-amylase 2) was detected in the maternal tissues, prior to anthesis, whereas α-amylase 3 was identified at a later stage, about 11 days after anthesis, just before the level of low pI enzyme was at it maximum. Upon further development of the grain, α-amylase 3 disappeared more rapidly than α-amylase 2.

An experiment by Marchylo *et al.* (1981) showed that the immature wheat endosperm-aleurone (seed coat and endosperm detached) produced considerably less α-amylase activity than immature whole or de-embryonated wheat kernels. They proposed that the seed coat may contain factor(s) required for normal α-amylase isozyme synthesis.

V.1) α-Amylase in Germinating Grain of Wheat

In the mature wheat grain germinative α-amylase appears after 2 days' imbibition, and steadily increases in amount with time (Kruger, 1972*b*). The sites of production of α-amylase in germinating grains have been investigated extensively in barley. It is generally accepted that gibberellic acid produced by the embryo of germinating barley acts upon the aleurone tissue to induce the *de novo* synthesis of several hydrolases, including α-amylase (Paleg, 1960; Groat and Briggs, 1969).

Varner and Chandra (1964) postulated that gibberellic acid controlled the synthesis of α-amylase (and other heat-stable proteins) in barley aleurone cells by causing the production of specific messenger RNAs. Recent studies, using cDNA hybridization techniques, have shown that GA_3 regulates the production of α-amylase mRNA in barley aleurone layers (Jacobsen and Higgins, 1982; Chandler *et al.*, 1984; Jones and Carbonell, 1984; Deikman and Jones, 1986).

Futher, calcium ions have an important role in synthesis and/or secretion of the high pI α-amylases (Jones and Jacobsen, 1983; Jones and Carbonell, 1984; Deikman and Jones, 1986). For instant Jones and Jacobsen (1983) reported that the withdrawal of Calcium ions from the incubation medium of barley aleurone layers reduced the rate of accumulation of α-amylase activity in the medium after 5 hours incubation by 85 % relative to controls incubated in the presence of 10 mM $CaCl_2$. The effect Calcium ions on the secretion of α-amylase was largely on group B α-amylase (α-amylase 1).

In wheat, aleurone layers secreted α-amylase when incubated with GA_3 (Rowsell and Goad, 1964b; Laidman *et al.*, 1974). Some evidence also suggested that α-amylase may be synthesized in the scutellum of wheat kernels (Marchylo *et al.*, 1980b; Okamoto *et al.*, 1980). Okamoto *et al.* (1980) using the substrate-film technique showed that α-amylase in the germinating cereal grain first appeared in the region of epithelial cells of the scutellum and diffused into the endosperm tissue later. That the embryo/scutellum produces α-amylase has since been confirmed by several workers e.g. MacGregor and Matsuo (1982) and Cornford *et al.* (1987). However the embryo contributes only a small proportion of α-amylase synthesized in the germinating barley. Groat and Briggs (1969) reported that in barley the removal of embryo at any time after 3 days germination had no effect on the quantity of enzyme ultimately produced in the endosperm.

Eastwood *et al.* (1969) reported that the aleurone tissue isolated from the quiescent wheat grain contained a considerable quantity of α-amylase which is completely secreted when the tissue is incubated in aqueous media. The addition of either kinetin or gibberellic acid to the medium did not significantly increase the level of enzyme activity. But when the aleurone tissue is incubated first with kinetin and then with gibberellic acid , there is a two-fold increase in secreted α-amylase activity. The earlier work by Trevener and Laidman (1968) had showed that the extract of wheat starch (endosperm) induced the release of α-amylase from the aleurone tissue, which has been isolated as bran from the quiescent wheat grain. This led

Eastwood *et al.* (1969) to conclude that the starchy endosperm of wheat seemed to contain a compound which has cytokinin activity and which is responsible for the induction of essential metabolic processes in the aleurone cells.

VI) ENDOSPERM DEGRADATION

The endosperm of wheat is composed of cells that contain many starch granules embedded in a matrix of proteinaceous material (Bradbury *et al.* 1956[a]. The starch granules in wheat consist of small spherical, B type granules approximately 5-8 μ in diameter and large lenticular A type granules approximately 15-30 μ in diameter (Sargeant, 1980). Evers and Linley (1977) reported that the small-size granules formed more than one third of the total weight of starch.

Dronzek *et al.* (1972) observed that α-amylase began its attack in the aleurone layer and preferentially attacked large lenticular granules. As germination proceeded B type granules were also eroded but at a slower rate than the A type granules. The large granules were attacked at the groove and at localized sites on the surface. Once the surface was eroded, the degradation seems to move through the layers of the granule toward the centre. In small granules the enzyme entered the granule at one or two sites and then completely digested the interior core of the granule (Dronzek *et al.*, 1972). B type granules are richer in phospholipids than A-type granules which could account for their slower degradation (Meredith *et al.*, 1978).

Fincher and Stone (1974) have demonstrated that the protein matrix which adheres to the starch granules in wheat endosperm disappears after one day's treatment with gibberellic acid. This change, attributable to proteolytic enzymes, would increase the accessibility of starch granules to attack by α-amylase.

MacGregor and Matsuo (1982) reported that in barley and durum wheat degradation started at the ventral crease edge of the endosperm-embryo junction and moved along this junction to the dorsal edge.

This suggested that the site of initial α-amylase synthesis in germinating cereal grains is the embryo and not the aleurone layer. Marchylo and Kruger (1987) studied the degradation of the endosperm by using Scanning Electron Microscopy in four cultivars of wheat. They found that the starch granule and protein matrix degradation first occurred adjacent to the crushed layer of cells. The results also showed that the wheat cultivar with least dormancy, Idead, exhibited the largest degree of starch degradation, whereas RL4137 the most dormant cultivar, exhibited no degradation. Dronzek *et al.* (1972) reported that in the sprouted samples, the starch granules near the aleurone layer of the kernel were attacked more severely than the starch granules in the inner endosperm.

Mundy *et al.* (1984) reported the presence in wheat of an inhibitor of endogenous α-amylase, it also capable of inhibiting the bacterial protease subtilisin. This inhibitor has been known as wheat amylase subtilisin inhibitor. The inhibitor is protein with Mr approximate 20500 and pI approximate 7.2. The results of Mundy (1984) showed that the α-amylase inhibitor in barley was an ABA-induced protein and that it functions as an active mediator of amylase activity during the development and germination of barley seeds. Slack *et al.* (1979) reported that hordein was a major protein that limits the rate of starch breakdown during mashing of barley. Weselake *et al.* (1985) reported the presence of endogenous α-amylase inhibitor in various cereals including wheat, but the α-amylase inhibitor level in a cultivar resistant to sprouting (Columbus) was not abnormally high when compared to other cultivars. They concluded that this endogenous inhibitor did not contribute to sprouting resistance. However, they mentioned that the results could be misleading since the enzyme activity was based on the activity of barley α-amylase. Abdul-Hussain (1987) reported that proteins from sprouting resistant genotypes inhibited α-amylase in standard assays, but adding EDTA (edetic acid) to chelate Ca induced inhibitory activity in extracts of all genotypes. Chromatography identified 6 peaks of activity with molecular weight of 14-68 K Da. None of the inhibitors influenced the germination of excised embryos. He

concluded that proteinaceous α-amylase inhibitors interact with Calcium ions, but do not play a primary role in the control of sprouting, although they may have secondary effects on the process. Jones and Meredith (1982) found that purothionins can inhibit the activity of wheat α-amylase. When calcium chloride was included in the inhibition-incubation mixture containing β-purothionin, the amylase activity was not inhibited. In the absence of calcium chloride, inhibition occurred as before. They postulated that purothionins may act by controlling the availability of calcium to serve as a cofactor.

Although α-amylase is the enzyme most studied in cereal, there exist also other enzymes which may be more important in the earlier stages of endosperm degradation. Gordon *et al.* (1977) have reported that endosperm degradation had already started before α-amylase activity increased from the base level indicating that the initial degradation of the endosperm may not cause by α-amylase.

VII) GENETICS OF PREHARVEST SPROUTING

The genetic control of many characters related to preharvest sprouting of the grains is known. Included in the list are genes controlling grain coat colour, insensitivity to gibberellic acid and α-amylase synthesis. But how the effects of these genes act and/or interact to influence dormancy is not clear.

VII.1) Grain Coat Colour

Nilsson-Ehle in 1911 established that red vs. white grain in wheat is conditioned by alleles at three different loci, with red being dominant (Allan and Vogel, 1965). This was confirmed by Gfeller and Svejda (1960). The three genes controlling grain coat colour seem to act in an additive way in that each additional gene results in at least some intensification of the red colour (Shull, 1948; Baker, 1981). However, McEwan (1980) found that in the F_2 populations of wheat derived from the cross between Hilgeldorf 61 (a red grained

wheat cultivar) and Aotea (a white grained wheat cultivar) there was no association between intensity of red grain colour and dosage of red grain genes.

Monosomic analysis showed that genes for red grain coat colour in various genotypes of wheat are located on chromosomes 3A, 3B and 3D (Allan and Vogel, 1965; Metzger and Silbaugh, 1970). By intercrossing six red winter wheats, six different grain coat colour genes were established (Freed, 1972). Reitan (1980) experimented with an 8 x 8 diallel cross between eight red grained and white grained, sprouting resistant and sprouting susceptible cultivars. He scored grain colour visually on a scale 1 to 5. The diallel analysis showed that red grain coat colour is close to being fully dominant over white. The F_2 segregations indicated that at least five different colour genes were present in the parental cultivars used in the crosses.

Relationships between red grain colour and dormancy were suggested to be due to linkage or pleiotropism (Gfeller and Svedja, 1960; Everson and Hart, 1961). Gale (1989) supported the idea that grain coat colour and dormancy are the results of pleiotropic effects of the genes, based on the lack of evidence which shows recombination between "linked" genes. McEwan (1980), experimenting with a wheat cross Hilgeldorf x Aotea, recommended that a high level of sprouting resistance can be conferred by single red grained gene in the homozygous condition.

VII.2) GA Insensitivity

A single gene conferring GA insensitivity was located on chromosome 4A (Gale and Marshall, 1975, 1976; Gale *et al.*, 1975a). The relationship between GA insensitivity and height reduction was of interest to plant breeders. By crossing tall x "Tom Thumb" type wheats, Gale and Marshall (1976) concluded that the reduced height gene (Rht_3) and GA insensitivity gene (Gai_3) either had extremely tight linkage or, more probably, were in fact the same gene. They also found that the Rht_1 and Rht_3 are alternative alleles at the same

locus. Gale (1989) has recently given a brief review on GA insensitivity gene in wheat. Five Rht alleles are now known in wheat. Rht_1 and Rht_2 are the Norin 10 semidwarfing genes which have been widely exploited in commercial cultivars. The "Tom Thumb" dwarfing gene, Rht_3 allele, is the most potent, and conferred the dwarfness of plant type which was considered too short for use in cultivation. Effects of Rht_1 and Rht_3 were compared in monosomic lines by Lenton and Gale (1987). While Rht_1 can reduce α-amylase levels, Rht_3 nearly eliminates α-amylase at maturity. Norin 10 is one of the ancestors of many semidwarf cultivars including Sonora 64, while in Tom Thumb dwarfness was introduced into a number of cultivars including the spring wheat Tordo (Lelley, 1976).

VII.3) α-Amylase Genes

Gale (1989) made an extensive review on the genetic control of three types of α-amylase in wheat. The first group of α-amylase is α-amylase 1 or malt amylase, consists of 7-14 isozymes controlled by α-AMY-1 genes which located on three compound loci on the long arm of chromosomes 6A , 6B and 6D. Each locus controls the production of more than one isozyme. The second group, α-amylase 2 or green amylase, is controlled by genes on three compound loci on chromosomes 7AL, 7BL, and 7DL. The third group reported by Daussant and Renard (1987) (α-amylase 3) is controlled by α-AMY-3 gene on group 5 chromosomes.

VII.4) Inheritance of Dormancy and Preharvest Sprouting Characters

Heritability of grain dormancy in wheat was reported to be as high as 73 - 76 % (Gfeller and Svejda, 1960, Reitan, 1980). Gordon (1978) reported high heritabity for grain colour, harvest ripeness and anthesis date; medium high heritability for net germination, damage score, grain weight at harvest, embryo dormancy and embryo maturity; and low heritability for base α-amylase and germinative α-amylase. In a diallel analysis of five wheat cultivars, Gordon (1987) found

that dormancy and germination had specific combining ability (s.c.a) as their main source of variation. The s.c.a heritability for dormancy and germination were 58.8 and 56.1 % and the general combning ability heritability (g.c.a heritability) for these characters were 2.0 and 2.3 % respectively.

VIII) GENERATION MEAN ANALYSIS

The generation mean analysis is used to study gene effects by using different generations derived from a cross between homozygous parents. The analysis aims to detect the effects of specific types of gene action and to estimate the contribution of a particular component to the overall variation (Snape, 1987).

The most common experimental structure in wheat is to use the early filial generations derived by intercrossing and selfing the parents and their F_1s. This produces six generations: P_1 (the higher score parent), P_2 (the lower score parent) , F_1, F_2, B_1 (backcross of the F_1 to the higher score parent) and B_2 (backcross of the F_1 to the lower-score parent). More complex experiments can be produced by the inter crossing and selfing these generations further (Snape, 1987).

Hayman (1958) proposed that if the two inbred lines differ by any number of unlinked genes the expectations of their, and some of their descendant, family and generation means may be expressed as

P_1	$= m + d$	$- (1/2)\ h$	$+ i$	$- j$	$+ (1/4)\ l$
P_2	$= m - d$	$- (1/2)\ h$	$+ i$	$+ j$	$+ (1/4)\ l$
F_1	$= m$	$+ (1/2)\ h$			$+ (1/4)\ l$
F_2	$= m$				
B_1	$= m + (1/2)\ d$		$+ (1/4)\ i$		
B_2	$= m - (1/2)\ d$		$+ (1/4)\ i$		
F_3	$= m$	$- (1/4)\ h$			$+ (1/16)\ l$
B_1S	$= m + (1/2)\ d$	$- (1/4)\ h$	$+ (1/4)\ i$	$- (1/4)\ j$	$+ (1/16)\ l$
B_2S	$= m - (1/2)\ d$	$- (1/4)\ h$	$+ (1/4)\ i$	$+ (1/4)\ j$	$+ (1/16)\ l$
F_4	$= m$	$- (3/8)\ h$			$+ (9/64)\ l$

i.e. $\text{mean} = m + \alpha d + \beta h + \alpha^2 i + 2\alpha\beta j + \beta^2 l$

P_1 and P_2 are the means of the two parent families and F_1 is the mean of their progeny. F_2, F_3 and F_4 are the means of the generations descending from this cross by selfing. B_1 and B_2 are the means of the two backcrosses. B_1S and B_2S are the means of the progeny of selfing the first two backcross families.

The genetic parameters d , h, i, j , l have the folowing meanings:

d = pooled additive effects;

h = pooled dominant effects;

i = pooled interactions between additive effects;

j = pooled interactions between additive and dominance effects and

l = pooled interactions between dominance effects.

When more than one loci are involved in the character under consideration, the increasing alleles may occur together in one of the true breeding parents and the decreasing alleles in the other. In this case the distribution of the genes are associated. On the other hand if each parent caries the increasing allele of one gene and the decreasing allele of the other, the distribution of the genes are in the dispersion state (Hayman and Mather, 1955; Mather and Jinks, 1971). Under the dispersion state the genes tend to balance one another out, so the additive effect is the sum of additive effects at all loci, taking sign into account. Similarly the dominant effect , is the sum of dominant effects of individual genes taking sign into account. But for dominant effect the sign of "h" does not depend on gene association nor dispersion but on the direction of the dominance itself (Hayman and Mather, 1955; Mather and Jinks, 1971). Snape (1987) pointed out a problem in interpreting the analysis of generation means in that the effects are the balanced effects of all segregating loci.

Gamble (1962) used the symbols "*a*" for additive effects, "*d*" for dominance effect, "*aa*" for additive by additive interaction, "*ad*" for additive x dominance interaction, and "*dd*" for dominance x dominance

interaction. The parameters for the various gene effects used by Gamble (1962) can be related with those used by Anderson and Kempthorne (1954) and by Hayman (1958) as follows:

Gene effect	Gamble	Anderson and Kempthorne	Hayman
Mean	*m*	K2	m
Additive	*a*	E + F	d
Dominance	*d*	2E	h
Additive x additive	*aa*	G + L + M	i
Additive x dominance	*ad*	2G + L	j
Dominance x dominance	*dd*	4G	l

Anderson and Kempthorne (1954) set the genetic assumptions in the development of their genetic model as follows:

1) multiple alleles absent;
2) linkage absent;
3) lethal genes absent;
4) constant viability for all genotypes and
5) environment effects additive with genotypic value.

Assumption 5 could hardly be valid in many experiments when genotype x environment interaction is important. The use of population means averaged over environments will reduced the bias in estimates the gene effects (Gamble, 1962).

When genotype x environment interaction exists, the model for generation means can include new parameters. The parameters are

e = environmental effects;
ae = additive x environment effect;
de = dominance x environment effect;
aae = (additive x additive) x environment effect
etc.

Mather and Jinks (1971) expressed the expected generation means with a model similar to the model proposed by Hayman; but using F∞ generation, which is the population of all inbred lines derived from the cross of two inbreds, as a background mean instead of the F_2 generation.

Generation mean analysis has been widely used to estimate the genetic parameters for various characters in many crops. In wheat it has been used to study the inheritance of photoperiod response and vernalization response (Klaimi and Qualset, 1973, 1974) , the inheritance of kernel weight (Bhatt, 1972; Sun *et al.*, 1972); to study gene effects for heading date and plant height (Amaya *et al.*, 1972; Bhatt, 1972; Edwards *et al.*, 1976; Ketata *et al.*, 1976), yield and yield components (Chapman and McNeal, 1971; Amaya *et al.*, 1972; Edwards *et al.*, 1976; Ketata *et al.*, 1976), and grain protein (Chapman and McNeal, 1970) ; and to estimate the gene effects for α-amylase in the wheat grains (Gale, 1976).

Gale (1976) proposed the model for generation mean analysis of GA_3-induced α-amylase in the wheat grain. His model considered the inheritance of this character in triploid scale. The main difference in the endosperm model (or triploid scale) from the diploid model is that heterozygotes can deviate from the mid-parent even in the absence of dominance, and that there are two distinct intra allele interaction components, "h_1" and "h_2". The two models are presented in Figure 2.

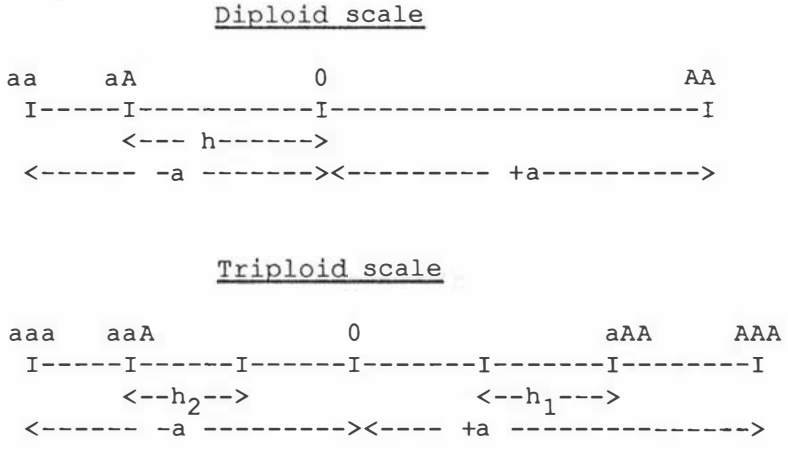

Figure 2. The genotypic values of the homozygotes and the heterozygotes based on diploid and triploid scale. (After Gale, 1976).

The triploid model fitted the data better than the diploid model for GA_3 induced α-amylase (Gale, 1976).

IX) OTHER METHODS OF INHERITANCE STUDIES

IX.1) Diallel

An alternative approach in studying the gene effect is the diallel analysis. The method consist of crossing the lines in all possible combinations. The major purpose of these design is to detect and estimate the additive and dominance variance (Snape, 1987). The variance among families within an array of parents (V_R) and covariance among families within an array with their non recurrent parents (W_R) were computed. If there is no epistasis or no correlated gene distribution the graphical analysis of W_R/V_R can indicate the distribution of dominant and recessive genes among the parents. Hayman (1954) gave the genetic assumptions for genetic model as follows :

(i) diploid segregation;
(ii) no difference between reciprocal crosses;
(iii) independent action of non allelic genes (no epistasis).

In a diallel cross the additional assumption are:

(iv) no multiple allele;
(v) homozygous parents;
(vi) genes independently distributed between the parents.

Assumptions (iii) and (vi) have been under scrutiny by Gilbert (1958) and Baker (1978). The untenable assumption (vi) leads to overestimation of the average level of dominance. Also the presence of epistasis affected estimates of general and specific combining ability, mean squares, variances, and gene effects (Baker, 1978).

Griffing (1956) applied the concept of combining ability to the diallel data. Sprague and Tatum (1942) defined the term "Generaal Combining ability" as the average performance of a line in hybrid

combination, and the term "specific combining ability" as the situation where certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved. General combining ability is primarily the result of additive gene action while specific combining ability is the expression of performance between any two inbred lines and is attributed to dominant, epistatic and additive gene action (Welsh, 1981).

There are four experimental methods in diallel analysis

(i) parents, one set of F_1's and reciprocal of F_1's are included

(ii) parents and one set of F_1's are included but reciprocal F_1's are not;

(iii) one set of F_1's and reciprocal are included but not the parents; and

(iv) one set of F_1's but neither parents nor reciprocal F_1's is included (Griffing, 1956).

In each of the experimental methods two models of analysis are available (a) a random effect model, where parental lines are considered as a random sample from population and (2) a fixed effect model, were parental lines are considered as fixed set of lines.

According to Griffing's (1956) model , the varities effects are considered in terms of general and specific combining ability effects, such that

$$V_{ij} = G_i + G_j + S_{ij}$$

for those diallele crossing methods in which reciprocal F_1's are not included, and

$$V_{ij} = G_i + G_j + S_{ij} + R_{ij}$$

for methods in which reciprocal F_1's are included.

G_i is the general combining ability (g.c.a) effect of the i^{th} parents,

S_{ij} is the specific combining ability (s.c.a) effect for the cross between the i^{th} and j^{th} parents, and

R_{ij} is the reciprocal effect involving the i^{th} and j^{th} parents.

IX.2) Other Designs

There are a few of other designs of experiment to study the gene effects e.g. The North Carolina Design 3 (Comstock and Robinson, 1952), the F_2 Triple Test Cross (Kearsey and Jinks, 1968). Each design has some advantages over another in some respects. Some designs was implemented to investigate the effect of linkage e.g. the Recurrent Backcrossing (Hill, 1966).

CHAPTER 3

MATERIALS AND METHODS

In the previous chapter, much of the information related to grain dormancy and sprouting damage was reviewed. Despite the vast amount of information available, the cause of grain dormancy is still a mystery. Partly, this may be because the materials used in different experiments were different with respect to dormancy, but also the procedures used were different from experiment to experiment. Compared to the physiological information, the information on gene effects controlling sprouting resistance is quite scarce.

This series of experiments was carried out to investigate the effect of genes on grain growth, maturity and dormancy in different generations of wheat derived from three crosses and ripened in two environments.

Attributes related to grain growth and germination were monitored at intervals from a few days after anthesis until the grains reached maturity. The measured values were fitted to appropriate functions, using the numbers of days from anthesis as the independent variable. The timing of some critical events, e.g. time of 90 % maximum grain weight, were derived by back substitution from the fitted functions. The gene effects of preharvest sprouting attributes were estimated using Hayman's (1958) generation mean analysis.

The objectives of these experiments were:

1) to investigate the nature of gene effects controlling sprouting characters in wheat.

2) to study the effect of grain ripening conditions on the maturity and germinability of the wheat grains.

3) to establish the pattern of grain maturity in different grain ripening environments and its importance in determining germinability of the grains.

In order to obtain information on gene effects controlling sprouting characters generation mean analysis (section VIII in the Review of Literature) was used. Three wheat crosses from four cultivars of wheat were used to cover a wider range of genetic backgrounds. The parental cultivars and their descendants were grown in two different grain ripening conditions. Details are given in the following section.

I) CULTIVARS AND GENERATIONS

Six generations derived from each of three wheat crosses were used in the experiments. Each of the three crosses had Tordo, as a common parent, this being a white grained wheat, putatively resistant to preharvest sprouting. This cultivar has low sensitivity to exogenous gibberellin (GA_3) and has limited capacity to synthesize α-amylase on germination (McMaster, 1976). The other parents in the crosses were: Karamu, Gabo, and Sonora 64A. Karamu is a red grain wheat resistant to preharvest sprouting, Gabo is a white grain wheat, susceptible to preharvest sprouting and Sonora 64A is a red grain wheat susceptible to preharvest sprouting. Hereafter the cross between Tordo and Karamu will be referred to as cross 1, between Tordo and Gabo as cross 2, and between Tordo and Sonora 64A as cross 3.

The generations used from each cross are P_1, P_2, F_2, F_3, $BC_1(P_1)S_1$, and $BC_1(P_2)S_1$, where F_2 is the bulk selfed progeny of F_1, F_3 is the bulk selfed progeny of F_2. In this chapter and the following chapters the system of naming the backcross generations is different from the system used by Snape (1987) which was quoted in the previous chapter. The generation designated $BC_1(P_1)S_1$ is the first selfed progeny of the first backcross of F_1 to the first parent, which is Tordo. Similarly the generation designated $BC_1(P_2)S_1$ is the first selfed progeny of the first backcross to the second parent (Karamu in cross 1, Gabo in cross 2 and Sonora 64A in cross 3).

II) GENERATION ADVANCE

The generation advance was carried out in a glasshouse, commencing May 1984. Seven to ten F_1 plants from each cross were raised. Some of these F_1 plants were used to produce F_2 seeds, and others were used in the backcrossing to the parents. All the F_2 seeds from each of the F_1 plants in a cross were harvested. Details on planting medium and the fertilizer used in the generation advance are listed in Appendix 1.

About 100 F_2 plants per cross were grown, two per planting bag, in successive years. F_3 seeds from each F_2 plant in each cross were harvested separately. At the same time as F_2 was sown, the backcross generations were sown for each cross. The selfed seeds of $BC_1(P_1)$ and of $BC_1(P_2)$ were bulk harvested separately. Also a few plants of parental generations were sown at the same planting season to rejuvenate those generations.

From when the backcross seeds were obtained, one more season of sowing was required for each cross, to grow F_2 together with $BC_1(P_1)$ and $BC_1(P_2)$. From this sowing F_3, $BC_1(P_1)S_1$ and $BC_1(P_2)S_1$ seeds were obtained at harvest. The F_3, $BC_1(P_1)S_1$ and $BC_1(P_2)S_1$ seeds of cross 1 were obtained in December 1984, and those of the other two crosses were obtained in the following seasons.

Two randomized complete block experiments were conducted for each of the three crosses. One experiment of each pair provided cool ripening conditions, while the other provided the warm ripening conditions.

III) EXPERIMENTAL MATERIALS

- Raising the Experimental Materials

Before the booting stage, all the generations used in an experiment were grown in a controlled glasshouse. Two plants were grown in each 14 x 14 x 14 cm^3 plastic pot, for which the medium was

made of sand, peat and vermiculite in the proportion of 70:15:15 by volume. Seeds were pregerminated on Whatman filter paper, using 0.5 % KNO_3 solution as imbibant, under 15°C/20°C temperature and alternate dark/light period, before planting. The seedlings were transplanted into planting medium when most of the seeds had germinated (4 days after starting the germinating treatments). The environmental conditions in the glasshouse were: 20°C day temperature and 16°C night temperature with 14 hours daylength. The plants received about 100 cm^3 of North Carolina Solution (Appendix 2) per pot. Extra water was applied as needed.

Sowings of the segregating generations were staggered in three sowings at one week intervals. This practice was carried out with the aim of having F_2 and F_3 materials with similar growth stages at the time the plants were transferred into controlled climate rooms. However only a few plants from the early sowing could be used because most of them were more advanced in stage of growth than the plants that were sown at the same time as the parental generations. The total numbers of plants sown in the glasshouse varied among generations. Appendix 3.A shows the date of planting and numbers of pots planted in each of the six generations of cross 1. The numbers of pots planted for crosses 2 and 3 are presented in Appendix 3.B and 3.C. The plants were transferred into the two controlled climate rooms at the booting stage (Feekes scale 9 or 10).

IV) EXPERIMENTAL DETAILS IN THE CONTROLLED CLIMATE ROOMS

The design of the experiment in the controlled climate rooms was a randomized complete block with three replications. Each experimental unit consisted of 6 pots (12 plants) for P_1, P_2, $BC_1(P_1)S_1$ and $BC_1(P_2)S_1$, and 12 pots (24 plants) for F_2 and F_3 generations. Ears were tagged at the first anthesis, so that the age of the grains could be determined. Ears from the main culms (primary tillers) were tagged together with a few ears from secondary tillers.

The conditions in the controlled climate rooms were as follows:

IV.1) Temperature

In the warm environment, the temperatures were kept at 27°C/21°C day/night temperature whereas in the cool environment the temperature were kept at 18°C/12°C day/night. Day temperature and night temperature in each of the climate rooms lasted for 6 hours, each followed by 6 hours of gradual change.

IV.2) Light

The light intensity was 160 W m^{-2} with a 14 hour photoperiod, with an abrupt light-dark change over. Darkness coincided with the cooler phase of the temperature pattern.

IV.3) Nutrient

A hundred ml of North Carolina solution (see Appendix 2) were given to a pot through micro tubes 6 times a day. An additional 100 ml of water was given after nutrients application.

IV.4) CO_2

CO_2 level was maintained at an ambient level (331-431 ppm) throughout the experimental period. Air flow down through the plants was 0.3-0.5 m sec^{-1} as measured with an Alnor Instruments thermoanemometer.

IV.5) Insect and Disease Control

The insecticide "Attack" (active ingredients: 475 g/litre pirimiphos-methyl and 25 g/litre permithrin in the form of an emulsifiable concentrate) at the concentration of 1 ml/l was used to spray at intervals to kill aphids. One gram of fungicide "Benlate" (active ingradient is 50 % w/w benomyl in the form of wettable powder) was added into each litre of the insecticide solution to control powdery mildew. The sprayed volume was 4.5 litres per climate room.

V) SAMPLING OF THE EARS

Serial samples over the whole period of grain development were harvested from the tagged ears. Regression analyses of each variable (e.g. grain dry weight, germination percentages etc.) as a function of grain age (in days after anthesis) were done for each experimental unit. From these functions, the statistics were derived and used later in the generation mean analysis.

Four to five ears were sampled at 7 day intervals, starting from 7 days after anthesis in the warm environment and at 10 day intervals, starting from 10 days in the cool environment. Whenever posible ears that reached anthesis on the same date were used in the sample. The ages of the grain were expressed as the numbers of days after anthesis (DAA).

Ears were immediately deglumed using clean forceps. Only the grains from the middle two thirds of the ear were used, and only the grains at the positions of first and second florets in a spikelet were used for measurements. This restriction of the sampling area was to reduce variation in size and maturity of the grains, which is well known to vary with position (e.g. Rawson and Evans, 1970). Also this sampling would minimize ear variation in the time of anthesis among florets within the ear (Rawson and Evans, 1970). The confined sampling area of grains, combined with the anthesis tagging procedure make it possible to determine the sampled grain age accurately, to within ±1 day. This would enable a clear picture of the grain processes and values to be attained, without the masking effects of ear position and tiller cohort. Grains detached from the ears were stored over water in a humidifier pending further treatment.

VI) ATTRIBUTES MEASURED

The following attributes were measured from aliquots of the grain samples.

VI.1) Grain Dry Weight and Grain Moisture Content

A sample of ten grains was weighed immediately after removing the glumes. They were then put into oven at 60°C for 48 hours. The dry grains were reweighed, after cooling to room temperature in the desiccator for one hour. Grain dry weight was expressed in mg per grain. The grain moisture content was expressed as a percentage of fresh weight following usual cereal-technology practice.

VI.2) Harvest Ripeness

Harvest ripeness in the experiments was defined as the time when the grain moisture decreased to 12.5 %. This was estimated from the interpolation of cubic spline curve of grain moisture content (detailed in VII.1.1 this chapter).

VI.3) Standard Germination and Potential Germination

Each of two twenty grain samples was subjected to a different germination test. For standard germination, the grains were put crease down into a 9 cm. Petri dish on a Whatman filter paper, and 5 ml of distilled water added. Germination was carried out at 20°C without light (Anonymous, 1966).

Potential germination was evaluated as the germination when three mechanisms of dormancy breaking were applied, thereby reflecting mean ontogenic ability to germinate. Grains were put crease down into 9 cm Petri dish on a Whatman filter paper, the germination medium being 5 ml of 0.5 % KNO_3 solution. The Petri dish was then kept in a germination cabinet with alternating temperatures and light as follows : 16 hours of diffuse light at 20°C and 8 hours of darkness at 15°C. This method combines three of the reported procedures to break dormancy (Anonymous, 1966) and was first used in this context by Gordon (1975). It has since also been used successfully by Cross (1977) and Very (1978).

The number of germinated grains in both tests were counted after 5 days of incubation. Grains were considered as germinated when the embryo ruptured the pericarp. All the grains used in the germination

tests were assumed to be viable and no tetrazolium test for viability was carried out, as earlier experiments had shown that the number of non-viable grains was very small (Gordon, 1975; Cross, 1977). Germination was thus expressed as the percentage of germinated grains based on total grains used in the test.

VI.4) Grain Colour Score

Two to three grains were used for a colour score test. For the segregating generations (e.g. F_2 generation), one grain from each ear was used. A modified technique of Quartley and Wellington (1962) was used. Grains were soaked in 5 ml of 5 % NaOH for one hour, and compared with five standard cultivars, which had been treated similarly. The five standard cultivars, ranked from the lowest score (white) to the highest score (dark red), were:

1) New Zealand Velvet score = 1,
2) Spoetnik score = 2,
3) Pitic score = 3,
4) Park score = 4,
5) Hope score = 5.

The grains which had not yet developed colour, or where the chlorophyll colour of the pericarp was still present were scored as zero. In cases where the sample consisted of grains with varying colour scores, the mean colour score was recorded for later analysis.

The values of the colour score of each sample were adjusted by adding 0.5 to the score first, and then multiplying by 2. This results in 10 intervals of ordinal scores. The adjusted scores were then transformed into normal scores using Table IV of Bliss and Calhoun (1954). In the analysis these adjusted and transformed scores will be referred to as normal scores. It should be noted, therefore, that colour has been measured semi-quantitatively, and not qualitatively as in classical genetic studies. The division line between "white" and "red" is at about 2.5 -3.0 before normalisation.

VI.5) α-Amylase Concentrations

The activities of α-amylase were determined from three aliquots of grain samples, each aliquot being treated differently to assess varying aspects of amylase development. They were then dried in the oven at 60°C for another 48 hours. This dried sample was kept in cool storage pending assay.

VI.5.1) Base α-Amylase

This is the α-amylase from harvested-condition after drying in the oven at 60°C for 48 hours. The drying treatment used is known not to de-activate α-amylase (Barnes and Blakeney, 1974). To conserve material, the sample for this assay was the same as that used for grain dry weight. This represented the base, non germinative α-amylase in the grains.

VI.5.2) Germinative α-Amylase

A ten-grain sample was put into standard germination conditions for 48 hours, before drying as above. This α-amylase level reflected germinative α-amylase and from it "amylase maturity" would be defined with respect to the earliest time at which such amylase could be synthesised by the grain.

VI.5.3) Gibberellin α-Amylase

In experiment related to cross 1, a sample of ten grains was germinated in dark conditions for 48 hours at 20°C, with 10^{-5} M GA_3 as a germination medium. In crosses 2 and 3 the GA_3 concentration was increased to 10^{-4} M. This α-amylase level reflected the α-amylase of the grains which were promote by gibberellin. This treatment was implemented to investigate the GA sensitivity of the wheat genotypes on the one hand, and on the other hand to find out whether gibberellin will bring about earlier maturity or not.

The α-amylase determination was carried out using the method of Barnes and Blakeney (1974). The method is based on the colorimetric measurement of the product released from Phadebas tablets. The Phadebas tablet being a β-limit dextrin derived from potato starch which is labelled with Cibachron blue. It is α-amylase specific, being completely resistance to attack by β-amylase (Barnes and Blakeney, 1974).

After the sample extract had reacted with the Phadebas tablet, under standard conditions (50°C in a water bath for 15 minutes), the coloured supernatant was read for absorbance with a Spectrophotometer at 620 nm. The absorbance values were converted into EU/l of α-amylase activity by the standard curve accompanying the Phadebas tablets. One unit (EU) of α-amylase activity is defined as the amount of enzyme catalyzing the hydrolysis of 1 μmol glucosidic linkage per minute at 37°C. The α-amylase concentration was converted into ln ($mEUg^{-1}$) for regression analysis.

VII) DATA ANALYSIS

VII.1) Estimating Data from Regression Equations

The measurements of each variable across sampling times in each experimental unit were used as dependent variables in regression analysis using the age of the grains as the independent variable. Different regression equations were estimated for each experimental unit in each experiment. The estimated values of dependent variables at particular times, or the estimated times when a dependent variable attained a certain level, formed a new set of derived variables which were used later in subsequent analysis of variance and the generation mean analysis. In the few case where data of an experimental unit failed to fit the function, the data in that experimental unit was derived by either linear interpolation or was treated as a missing value.

VII.1.1) Moisture Content

Initially, two functions were tested with this character, the logistic and the modified logistic. The logistic function has been used successfully by Gordon (1975) and Cross (1977). In the present experiments even though both functions gave an acceptably high value of R^2, the estimated time of harvested ripeness usually fell out of range.

The logistic function has the form:

$$Y = 1/[1 + e^{(a-b \cdot X)}]$$

where Y = grain moisture content (%),
X = age of grains,
a and b = unknown parameters,
e = base of natural logarithm.

And the modified logistic function has the form:

$$Y = b + a/[1 + e^{(c - d \cdot X)}]$$

where Y and X are grain moisture content and age of grains as before, a, b, c, and d are unknown parameters.

Because moisture contents are values which can be measured with high accuracy, the estimated time of harvest ripeness from the logistic function or from modified logistic were considered unsatisfactory. The spline cubic function (Rice, 1969) was then used to express the change of moisture content along the x axis (age of the grains). Estimates of time to harvest ripeness were obtained from this spline cubic function, using the program "MC.EST.F77" (D.R. Smith, unpublished).

Spline functions are piecewise polynomial of degree n, that are connected together (at points called knots) so as to have n-1 continuous derivations (Rice, 1969).

The cubic spline, or the spline function of degree 3, has the formal algebraic definition as

$$S(x) = \sum_{j=0}^{3} a_j x^j + \sum_{t=1}^{m} (1/6) d_t (x - \xi_t)_+^3$$

where $(x - \xi_t)_+ = \begin{cases} 0, & \text{when } x \leq \xi_t \\ (x - \xi_t), & \text{when } x \geq \xi_t. \end{cases}$

In this formulation it was assumed that "knots" ξ_t, at which the separate pieces are jointed, are in the order, $\xi_1 < \xi_2 < \ldots < \xi_m$ (Powell, 1970).

VII.1.2) Grain Dry Weight

The grain dry weights were fitted to the Gompertz equation. This relationship has proved to be satisfactory (cf. Gordon, 1975; Cross, 1977). The equation used can be written as:

$$Y = a \cdot e^{-e^{(b - c \cdot x)}}$$

where Y = weight of grains,

x = age of grains expressed in days after anthesis,

e = based of natural logarithm,

a, b and c are the unknown parameters of the function. This function has an upper asymptote equal to "a". The point of inflection of the curve, i.e. the point when the slope of the curve changes, occurs when X equals a/e. In this equation parameter c is a rate parameter, a high value indicating a rapid rise of the function between the two asymptotes. The ratio b/c defines the value of X at the point of inflection (Causton and Venus, 1981).

The fitting of this function was affected by using the program "SIGMOID" (D.R.Smith, unpublished).

Derived variables obtained from the fitted curves were:

1) Grain dry weight at harvest ripeness (HRDW),

2) Maximum grain dry weight (MAXDW), and
3) Time at which the grains reached 90 % of their maximum dry weight (T90DW), and will be referred to as dry weight maturity.

The level of response at 90 % of the upper asymptote (90 % dry weight) was chosen as an arbitrary high level near to the maximum, bearing in mind that the estimates will have lower standard errors than estimates at higher levels (e.g. 95 or 99 %). This arbitrary level was also applied to other characters as well. It avoids the problem of x-axis attenuation near the Y-axis asymptote, and approximates field perception of the end of the process.

VII.1.3) Standard Germination and Potential Germination

The term "germination" implied the actual germination percentage observed under the standard germination test. The term "germinability" implied the net germination when dormancy had been bypassed, so it also measured the readiness of the embryo to germinate, i.e. measured embryo maturity (Gordon, 1975; Cross, 1977)(see also section VI.4, this chapter).

Changes in germination and germinability across time were described by the logistic function, as had been found also by Gordon (1975) and later used by Cross (1977). In these experiments the values of the germination percentages were transformed into a fractions of 1, and the upper asymptote was set as 1 (i.e. 100 %). Therefore the function can be expressed as:

$$Y = 1/[1 + e^{(a - b \cdot x)}]$$

where Y = percent germination in fraction of 1,
x = age of grains in days after anthesis,
a and b = unknown parameters.

The logistic function has a point of inflection half way between lower asymptote and upper asymptote. This makes the curve a symmetric sigmoid shape.

Derived data obtained from this function were:

1) time at which grains attained 50 % standard germination (T50SG), henceforth revered to as "median germination";
2) time at which grains attained 90 % standard germination (T90SG), henceforth referred to as "germination maturity";
3) time at which grains attained 50 % potential germination (T50PG), henceforth referred to as "median embryo maturity";
4) time at which grains attained 90 % potential germination (T90PG), henceforth will be referred to as "embryo maturity";
5) percent standard germination at harvest ripeness (HRSG); and
6) percent potential germination at harvest ripeness (HRPG).

VII.1.4) Estimated Dormancy Percentages

Dormancy percentages were estimated as the difference between the mean standard germination and potential germination of each generation in each environment. Gordon (1975) defined percentage embryo maturity as the germination percentage under dormancy breaking conditions. With the assumption that all the grains in the test were viable the percentage embryo maturity will be equal to the percent potential germination in this experiment. Also he defined dormancy as the inability to germinate caused by specific processes resulting in the mature embryo (i.e. apart from immaturity). By these definitions dormancy may be estimated by:

$$\text{Dormancy (\%)} = \frac{100(\text{potential germination} - \text{standard germination})}{\text{potential germination}}.$$

When the potential germination equals zero (or was not significantly different from zero in some cases), which means the embryo is immature, the dormancy will be undefined (missing data) (Gordon, 1975).

Full dormancy occurs whenever the standard germination is zero, and potential is non-zero. There were some occasions when potential germination had smaller value than standard germination which is the

problem attributable to independence of the random errors in the two measurements. In this situation the difference between potential and standard germination is set to zero and consequently the dormancy will equal zero (or, if potential germination was not significantly different from zero, remains undefined).

VII.1.5) Grain Colour Score

The grain colour scores, after transformation into the normal scores were fitted with logistic and modified logistic functions. Data from many experimental units failed to fit the logistic function, but they were described satisfactorily by the modified logistic function as judged by the high R^2 (Figures A.43-A.46). So this function was chosen to regress the normal colour score against grain age.

The modified logistic has the equation:

$$Y = b + a/[1 + e^{(c - d \cdot x)}]$$

where Y = the grains' normal colour score,

x = age of the grains in days after anthesis,

e = base of natural logarithm,

a, b, c, and d are unknown parameters.

Derived data from the curve fitting are :

1) Maximum colour score (MAXCOL), which is the asymptote of the modified logistic function,
2) time at which grains attained 90 % maximum colour score (T90COL), "grain colour maturity".

The colour scores at harvest ripeness, or at T90SG are usually equivalent to the maximum colour scores, so only the maximum colour score has been presented.

VII.1.6) α-Amylase Data

VII.1.6.1) *Base α-Amylase*

The pattern of change in the content of base α-amylase across time can be expressed as a quadratic exponential function (Gordon, 1975; Gordon *et al.*, 1979). The regression function can be written in the exponential form as:

$$Y = e^{[a + b(X) + c(X)^2]}$$

where Y = base α-amylase concentration in mEU/g,
X = age of grains in days after anthesis,
a, b, and c are unknown parameters of the equations.

The function can be simplified by taking the natural logarithm of the above equation which will result in :

$$\ln(Y) = a + b(X) + c(X)^2$$

This second form of equation is in the form of a second order polynomial equation, and was used in calculation. From this regression the estimates for values of base α-amylase at harvest ripeness and at T90SG were derived, by substituting x with appropriate values.

VII.1.6.2) *Germinative α-Amylase and GA3-induced α-Amylase*

These two variables have the patterns of change across grain ages that fall distinctly into two phases (Gordon, 1979b). The first phase has the same function as for base α-amylase i.e.

$$\ln(Y) = a + b(X) + c(X)^2$$

where X = age of the grains.

The second phase has the regression function as

$$\ln(Y) = a' + b'(X)$$

The two phases of the α-amylase concentrations are concurrent with biological expectations (Gordon, 1979b). Phase 1 represents the usual decline in pericarp activity in young grains; and phase 2 represented the response to germinative conditions in the endosperm (Olered and Jönsson, 1970; Kruger, 1972a ; 1972b; Olered, 1976). The intersection of the two phases are called phase intersect 1 (PI1) for the germinative α-amylase and phase intersect 2 (PI2) for the GA_3-induced α-amylase. The jointed fit regressions were carried out by using assigned dummy variables and were effected by procedure "REG" of the SAS program (SAS Institute,Inc., 1985).

The intersection point can occur at several points along the X-axis, depending on how the dummy variables were assigned (i.e. the initial allocation of the observed values to each phase). The criteria to judge which intersection is the better or more realistic choice are:

1) the intersection point should occur when the value of α-amylase is relatively low;
2) the intersection point should not cause overlapping between phases; and
3) the coefficient of determination (R^2) for the joined fit is relatively high.

A few jointed fit regressions were tried for each experimental unit. The jointed fit regression which satisfied the above criteria was chosen as the appropriate function.

Derived variables from these fitted curve were:

1) phase intersect 1 (PI1), henceforth called amylase maturity, being that point in time at which competency to produce germinative α-amylase occurs;
2) phase intersect 2 (PI2), henceforth called GA amylase maturity;
3) germinative α-amylase at HR;
4) germinative α-amylase at T90PG;

5) GA_3 α-amylase at HR; and

6) GA_3 α-amylase at T90PG.

A summary of the variables and their abreviated names are presented in Appendix 4 .

VII.2) Analysis of Variance

The analysis of variance for each cross was carried out separately, using procedure "GLM" of the SAS statistical package (SAS Institute Inc., 1985). In each of the three crosses, analysis of variance was effected for each environment, and also for the combined environments. A test for homogeneity of error variances between environments were carried out by using the Bartlett λ^2 test (LeClerg *et al.*, 1962). The results of the test are presented in Appendix 7. The combined analysis of the experiments which have different error variances will result in a loss of sensitivity in tests of significance (Cochran, 1947). The variables in the analyses are those variables derived from the regression equations. The model for analysis of variance in a single environment can be expressed as follows:

$$Y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij} \quad \ldots\ldots\ldots (1)$$

where Y_{ij} = the observed value of the variable under consideration of the i^{th} generation, in the j^{th} block,

μ = the mean common to all observations,

α_i = the effect of the i^{th} generation,

β_j = the effect of the j^{th} block.

ε_{ij} = the random error associated with the individual observations.

The significance of generation or block effects was tested by the usual F-test.

For the combined analysis of variance from both environments, the random effects model was applied, that is both generation and environment effects were considered as random samples of generations and environments. The model can be written as follows:

$$Y_{ijk} = \mu + \alpha_i + \beta_{j(k)} + \gamma_k + \alpha\gamma_{ik} + \varepsilon_{ijk}.$$

where Y_{ijk} = the observed value of the variable under consideration of the generation i^{th}, in the j^{th} block grown in the k^{th} environment.

μ = the mean common to all observations.

α_i = the effect of the i^{th} generation,

$\beta_{j(k)}$ = the effect of the j^{th} block within the k^{th} environments,

γ_k = the effect of the k^{th} environment,

$\alpha\gamma_{ik}$ = the interaction of the generation i^{th} with the k^{th} environment.

ε_{ijk} = the random error associated with the individual observations.

The appropriate F-tests for the generation effect is

$$F = MS\ (G)\ /\ MS\ (G.E).$$

Procedure "GLM" of SAS does not give the complex F-test nor degrees of freedom for environment effect. So the environmental effect was tested by the "THWAITE" program (I.L. Gordon, unpublished). The appropriate F-test for environmental effect is:

$$F' = [\ MS\ (EN) + MS\ (E)]\ /\ [MS\ (BLK) + MS\ (G.E)]$$

where MS (G) = Mean square for generation,

MS (G.E) = mean square for generation x environment interaction,

MS (EN) = mean square for environment, and

MS (BLK) = mean square for block (environment).

The degrees of freedom for the numerator and denominator in the F-test for environment effects are calculated according to Satterthwaite's (1946) equation:

$$f' = \left(\sum_{i=1}^{k} a_i MS_i \right)^2 / \left[\sum_{i=1}^{k} (a_i MS_i)^2 / f_i \right]$$

where f_i is the degrees of freedom associated with MS_i, the i^{th} mean square in the linear function, and $a_i = 1$ in this usage.

The expectation of mean squares for the single analysis of variance and for combined analysis of variance, given all the effects are random, are presented in Appendix 5 and 6 respectively.

The SAS type II sum squares were used for all characters. The type II sum squares based on the "Fitting Constants Method", in which the adjusted sum of squares are used to test for main effect (Speed, *el al.*, 1978). The least square means obtained from the analysis were used instead of the means. Least square means are the expected values of class or subclass means which would be expected for a balanced design involving the class variable with all covariates at their mean value (SAS Institute, Inc., 1985). This was done to accommodate the imbalance arising from missing data.

VII.3) Generation Mean Analysis

The generation mean analysis was carried out when the analysis of variance indicated significance for generations or generation x environment interaction. Principles of the method had already been reviewed in section VIII of Chapter 2.

The analysis incorporated epistasis and environmental effects in the model. The phenotypic value of any generation in any environment may be expressed, using Gamble's (1962) notation, as:

$$Y_{ik} = m + \alpha a + \beta d + \alpha^2 aa + 2\alpha\beta ad + \beta^2 dd + \gamma e + \alpha\gamma ae + \beta\gamma de + \alpha^2\gamma aae + 2\alpha\beta\gamma ade + \beta^2\gamma dde$$

where Y_{ik} = the phenotypic value of the mean of generation i in environment k.

m = background mean, which equal the mean of the F_2 generation, α, β, and γ are coefficients of corresponding parameters, as explained earlier (See also section VIII of Chapter 2). The coefficient γ was assigned value of +1 for the environment with higher expression and -1 for environment with lower expression. The parent with higher expression was set as P_1 throughout.

The terms *a*, *d*, *aa*, *ad*, and *dd* are the net gene effects as previously described (average allele, dominance, and three types of epistasis). The parameter *e* is the environmental effect. The last five parameters in the above equation are the interactions between genetic effects and environmental effects, They are *ae*, *de*, *aae*, *ade*, *dde*. The equation can be expressed in matrix notation as:

$$\mathbf{Y} = \mathbf{C}\,\mathbf{M}$$

where **Y** is the vector of the means (least square means), with dimensions 12 x 1 ; **C** is the coefficient matrix of size 12 x 12 ;and **M** is the vectors of the parameter estimates, with dimensions 12 x 1 (the unknown). The **Y**, and **M** vectors and the **C** matrix are showned below.

Y

$$\begin{bmatrix} P_1 \\ P_2 \\ F_2 \\ F_3 \\ BC_1(P_1)S_1 \\ BC_1(P_2)S_1 \\ P_1' \\ P_2' \\ F_2' \\ F_3' \\ BC_1(P_1)S_1' \\ BC_1(P_2)S_1' \end{bmatrix}$$

M

$$\begin{bmatrix} m \\ a \\ d \\ aa \\ ad \\ dd \\ e \\ ae \\ de \\ aae \\ ade \\ dde \end{bmatrix}$$

C

1.0	1.0	-0.50	1.00	-1.000	0.2500	1.0	1.0	-0.50	1.00	-1.000	0.2500
1.0	-1.0	-0.50	1.00	1.000	0.2500	1.0	-1.0	-0.50	1.00	1.000	0.2500
1.0	0.0	0.00	0.00	0.000	0.0000	1.0	0.0	0.00	0.00	0.000	0.0000
1.0	0.0	-0.25	0.00	0.000	0.0625	1.0	0.0	-0.25	0.00	0.000	0.0625
1.0	0.5	-0.25	0.25	-0.250	0.0625	1.0	0.5	-0.25	0.25	-0.250	0.0625
1.0	-0.5	-0.25	0.25	0.250	0.0625	1.0	-0.5	-0.25	0.25	0.250	0.0625
1.0	1.0	-0.50	1.00	-1.000	0.2500	-1.0	-1.0	0.50	-1.00	1.000	-0.2500
1.0	-1.0	-0.50	1.00	1.000	0.2500	-1.0	1.0	0.50	-1.00	-1.000	-0.2500
1.0	0.0	0.00	0.00	0.000	0.0000	-1.0	0.0	0.00	0.00	0.000	0.0000
1.0	0.0	-0.25	0.00	0.000	0.0625	-1.0	0.0	0.25	0.00	0.000	-0.0625
1.0	0.5	-0.25	0.25	-0.250	0.0625	-1.0	-0.5	0.25	-0.25	0.250	-0.0625
1.0	-0.5	-0.25	0.25	0.250	0.0625	-1.0	0.5	0.25	-0.25	-0.250	-0.0625

The solution for the parameter estimates was obtained by the inversion of matrix **C**, and post multiplication by vector **Y**, expressed in matrix form as:

$$\mathbf{M} = \mathbf{C}^{-1}\,\mathbf{Y} \qquad (1).$$

The inversion and multiplication of the matrix was carried out by the "MINITAB" program (Bray and Lai, 1987). Because the mean in each generation was obtained on a plot basis, no plant to plant variation (within plot variance) was available. This caused a problem in computing the variances or standard errors of the parameter estimates. If the plant variance of each generation were known, the variances of the parameter estimates can be computed as a linear function of those generation variances.

Since no within plot variances were available, the variance of the means (Least square means) was used as a basis for the variances of parameter estimates. However, to adjust the single variance of the means to reflect the expected variations on a plant to plant basis, the expectation of generation variances based on a simple gene model (non-epistasis, no genotype x environment interaction) was computed.

The expectations of genetic variances in each generation (Strickberger, 1976) were as follows:

$V(P_1) = E$

$V(P_2) = E$

$V(F_1) = E$

$V(F_2) = 1/2\ (a^2) + 1/4\ (d^2) + E$

$V(B_1) = 1/4\ (a^2) + 1/4\ (d^2) + E$ etc.

Likewise the expected variance of F_3 and selfed backcross will be

$V(F_3) = 3/4\ (a^{2)} + 3/16\ (d^{2)} + E$

$V[BC_1(P_1)S_1] = 1/2\ (a^2) - 1/16\ (ad) + 3/16\ (d^2) + E$

$V[BC_1(P_2)S_1] = 1/2\ (a^2) - 1/16\ (ad) + 3/16\ (d^2) + E$

Notice that the variances of $BC_1(P_1)S_1$ and $BC_1(P_2)S_1$ have the same expectations.

Strickberger (1976) defined environmental variance (E) in the above equations as the variation among identical genotypes of all individuals in an experiment. This means that the environmental variance (E) in the formula of Strickberger is equal to the variance of the generation means in these experiments.

The parameters estimated from the solution $\mathbf{M} = \mathbf{C}^{-1}\mathbf{Y}$ were used in computing the variance of parameter estimates. To adjust the generation variances for each environment another weighting was introduced. The environment weights were the proportions of error variance in that particular environment to the error variance from the combined analysis. The final adjusted variances were used as a $\mathbf{V}$ matrix in equation (2).

Error variances and covariances of the parameter estimates were computed as:

$$VAR(M) = (C'V^{-1}C)^{-1} \qquad (2).$$

Where **M** is the vector of parameter estimates,

V is the diagonal matrix of adjusted error variances,

V^{-1} is the inverse matrix of **V**, **C'** is the transposed coefficient matrix.

CHAPTER 4

RESULTS

I) TIMING OF EVENTS DURING GRAIN DEVELOPMENT AND RIPENING

I.1) Definitions

The names and abbreviations of the estimated variables may be summarized as follows:-

1) harvest ripeness(HR),

2) amylase maturity (PI1),

3) GA-amylase maturity (PI2),

4) median germination, or time to 50 % standard germination competency (T50SG),

5) germination maturity, or time to 90 % standard germination competency (T90SG),

6) median embryo maturity or time to median potential germination (T50PG),

7) embryo maturity (T90PG),

8) dry weight maturity (T90DW),

9) grain colour maturity (T90COL).

Each variable measured has a special connotation in relation to maturity and ripening of the grains. Further details have already been presented in Materials and Methods. Harvest ripeness (HR) is grain maturity in terms of moisture content,(12.5% moisture content in this experiment), and is useful for field applications. It represents a general definition of when the grain is firm enough for combine harvestings (Gordon *et al.*,1979; Picket, 1989). Phase intersect 1 (PI1) is the time when the decreasing phase of α-amylase ends and the increasing phase of α-amylase begins; and probably represents the point in grain maturity at which the capacity to produce α-amylase 1 exceeds the capacity to produce α-amylase 2 under germinative conditions. This variable can be interpreted as "amylase maturity"

VARIATIONS OF SOME DERIVED DATA

I. HARVEST RIPENESS.

Harvest ripeness was estimated from cubic spline fits to observations in each experimental unit.All fits were acceptable with respect to the estimations of the time at which the moisture decreased to 12.5 % (The chosen definition of Harvest Ripeness, proposed by Gordon(1979)). These harvest ripeness values always bounded by two neighboring obsevations, i. e. no estimates were marginal nor extrapolations. Some observation values of the moisture were perhaps suspicious e.g. the very low value of 3.05 % at 49 days after anthesis (DAA) in block 1 of Figure A.1.B., and the unusually high value of 22.98 % at 63 DAA in block 3 of Figure A.3.B. However all values were used as observed to the curve fitting, So there may be distortion of some estimates of harvest ripeness in those experimental units. But this practice has little effect on the mean for the treatments because of compensation by the values in other blocks. The block mean square may have been increased as may have been error.

In some of the experimental unit the number of plants was limited. It was necessary to spread the samples over a longer period, thereby widenning the interval between some samplings. Consequently, the spline cubic function for the data in that particular block may not be similar to other blocks for the same generation. This widenning of the interval was prominent in some backcross-selfed generations. For example in Figure A.3.E and A.3.F the first observation of block 2 start at about 7 days after anthesis and the second observations are at about 35 DAA. The same problem was found also in Figures A.4.A, A.4.B,A.5.B,A.5.E and A.5.F. These "gaps" are very early in the development sequence, and have affected the shape of the fit there. However, the observations are more concentrated near the harvest ripeness end of development, so that the curves are not displaced in this region. For this reason, it is unlikely that bias in harvest ripeness estimates has arisen from the wide sampling gaps. In future work, the experimental design should be modified to allowed for more plants per unit in the phytotrons.

II. EXTRAPOLATION OF AMYLASE DATA

The base α-amylase, germinative α-amylase and GA_3 α-amylase at embryo maturity of the cultivar Tordo were unusually high as has been mentioned on page 98. This was due to the lateness of estimated embryo maturity,resulting in an extrapolation of amylase beyond the window of curve fitting.This is not recommended,but the general attitude in these results has been to let all estimates stand as stochastic samples. Therefore, deletion on "outliers" has not been practiced. However, some estimates of amylase levels at embryo maturity in Tordo were so questionable that they were excluded from the Table (Table 23). Nevertheless they were included again in the pooled analysis of variance because analysis of variance cannot proceed if a treatment is missing entirely in one experiment among several. The results of this analysis need to be treated with caution as noted on page 98, and give only approximate indication of significance. However the genetic analysis of these estimates in cross 1 was not carried out.

for these amylase data were carried out and the result of the analysis were treated with caution (page 98).

and this term will be used synonymously with PI1. Phase intersect 2 (PI2) occurs when grains, treated with GA3 instead of water for two days, begin to show competency to produce α-amylase 1. This variable will be named "GA amylase maturity" to differentiate from amylase maturity.

T50SG is the number of days after anthesis when 50% of the grains show competency to germinate under standard conditions. T50PG is similar, except that the germination conditions are now designed to break dormancy (see Materials and Methods, section VI.4). T90SG and T90PG are the variables related to the readiness of 90 % of the grains to germinate under standard or dormancy breaking conditions respectively. As such, the latter variable may be considered as an index of embryo maturity in terms of its competency to germinate. The 9^{th} decile has been preferred over the median to define "maturity", as it is more akin to the field perception of when these events have occur.

T90DW is the time when the grain reaches 90 % maximum dry weight, and is similar to the conventional concept of so called "physiological maturity". In this discussion this variable ,T90DW, will be referred to as "dry weight maturity" which seems preferable. T90COL is the time when grain colour reaches 90% of it maximum value and will be referred to as grain colour maturity.

I.2) Cross 1's Results

Changes in grain moisture during ripening of the six generations of cross 1 wheat, Tordo x Karamu (GA insensitive x red, dormant),in the warm and cool environments are graphically presented in Figure A.1 and Figure A.2 respectively. The times in number of days from anthesis for nine events for cross 1 are presented in Table 1. The cool environment significantly delayed harvest ripeness, median embryo maturity (T50PG) and all other maturities (amylase maturity, GA-amylase maturity, embryo maturity, dry weight maturity and grain colour maturity).

RANDOM EFFECTS VS. FIXED EFFECTS

While these experiments considered generations and environments as random effects it may be argued that the two effects could be considered as fixed effects. If the two effects were fixed while the block effect was random, the expectation mean squares would change. According to Schultz (1955) the generation x environment component of variance will not exist in the expectation of the mean square of the generation and the environment but it will exist in the generation x environment mean square. As a result the F-ratios to test the environment effect and the generation effect (McIntosh, 1983) would be :

$$F_{(environment)} = \frac{MS(environment)}{MS(block)}$$

and

$$F_{(generation)} = \frac{MS(generation)}{MS\ (error)} \ .$$

Consequently, probabilities for F-test estimates for environment and for generation may change from those for the random effect model, as reported in the thesis. But the F-test for the generation x environment interaction effects would be the same. These mixed model F-ratios were investigated in some characters for comparative purpose. The significant symbols for the mixed model (generation and environment fixed, block random) are presented beside significance symbols of the random effects model in Table 1,2,4,5,7 and 8.

It is conceivable that under mixed models the sensitivity of the test is higher compared to random effect model. In contrast, the random model test is more rigorous and is more conservative. To decide which model is appropriate is an a prior decision before data analysis. It depends in part on the definition of the population of inference, an on whether the treatments are regarded as being exactly predefined without error.

Lindman (1974) has explained the difference between the random effects model and the fixed effects model as follows:

(1) In fixed effects model, the particular groups being compared have been chosen because they are of sole interest to the experimenter. With the random effects model, the groups being compared have been chosen randomly from a large population of potential groups.

(2) In random effects model the experimenter is interested in population variables, such as mean (μ), variance between groups ($\sigma^2_{between}$) and error variance (σ^2_e). There is no particular interest in specific comparisons between the randomly chosen groups. The advantage of the random effects experiment is that it enables the experimenter to generalize statistically beyond the groups (treatments) actually taken.

(3) To replicate a random effects experiment, one could choose a new random sample of groups from which to take observations. To replicate a fixed effect experiment one would obtain more observation from the same groups as used in the original experiment.

There were significant differences among generations for amylase maturity in the warm environment,but not in the cool environment. Averaged over the two environments, the two parental cultivars were not different from each other and the F_3 generation had significantly shorter amylase maturity compared with the two parents (Table 2). GA amylase maturity showed significant differences among generations only in the cool environment. The F_3 was the generation with the shortest GA amylase maturity.

The median germination (T50SG) and the germination maturity (T90PG) are presented for only five generations in the warm environment and for all generations in the cool environment. Estimates of median germination (T50SG) and germination maturity (T90SG) of Tordo in the warm environment were not available because the observed data did not fit the logistic function (Figures A.7 and A.9). Accordingly, the combined analysis of variance for these two characters was not conducted.

Among the seven characters related to ripening and maturity (variables in Table 2), dry weight maturity and grain colour maturity were the two earliest events, followed by amylase maturity and GA amylase maturity. Median embryo maturity (T50PG) and germination maturity (T90SG) occurred sometime later.

Paired t-tests for significant differences between maturity variables are presented in Table 3. Dry weight maturity and grain colour maturity were not significantly different from each other (Table 3). Harvest ripeness occurred close to amylase maturity and GA-amylase maturity, but these three maturity characters were all significantly different from each other.

Table 1. Estimated times of occurrence of harvest ripeness and other stages of grain development of Cross 1 (Tordo x Karamu) grown in two environments (in days after anthesis).

Generation	Harvest ripeness		Amylase maturity		GA-amylase maturity		Median germination		Germination maturity		Median embryo maturity		Embryo maturity		Dry weight maturity		Grain colour maturity	
									WARM ENVIRONMENT									
Tordo	41	(1.4)	39^{ab}	(3.9)	38	(2.5)	-		-		98^{a}	(3.7)	134^{a}	(9.0)	26	(6.7)	34	(2.4)
Karamu	42	(1.4)	44^{a}	(3.9)	36	(2.5)	-		-		42^{c}	(3.7)	50^{cd}	(9.0)	35	(5.3)	33	(2.4)
F_2	42	(1.4)	34^{b}	(3.9)	36	(2.5)	-		-		48^{c}	(3.7)	71^{bc}	(9.0)	35	(5.3)	32	(2.4)
F_3	41	(1.4)	33^{b}	(3.9)	32	(2.5)	-		-		41^{c}	(3.0)	48^{d}	(7.1)	33	(5.3)	32	(2.4)
BC_1(Tordo)S_1	43	(1.4)	33^{b}	(3.9)	32	(2.5)	-		-		59^{b}	(3.0)	87^{b}	(7.1)	40	(5.3)	33	(2.4)
BC_1(Karamu)S_1	42	(1.4)	39^{ab}	(3.9)	28	(2.5)	-		-		43^{c}	(3.0)	59^{cd}	(7.1)	25	(5.3)	32	(2.4)
mean	42	(0.9)	37	(3.1)	34	(4.6)	-		-		55	(5.1)	75	(13.0)	32	(9.7)	33	(3.5)
									COOL ENVIRONMENT									
Tordo	76	(1.4)	76	(3.9)	71^{a}	(2.5)	105	(2.9)	114	(6.8)	95^{a}	(3.0)	104^{ab}	(7.1)	60	(5.3)	61	(2.4)
Karamu	78	(1.4)	80	(3.9)	66^{a}	(3.2)	92	(2.9)	91	(6.8)	86^{bc}	(3.0)	92^{b}	(7.1)	57	(5.3)	62	(2.4)
F_2	76	(1.4)	74	(3.9)	67^{a}	(2.5)	98	(2.9)	102	(6.8)	98^{a}	(3.0)	118^{a}	(7.1)	51	(5.3)	61	(2.4)
F_3	74	(1.4)	63	(3.9)	58^{b}	(2.5)	97	(2.9)	111	(6.8)	90^{ab}	(3.0)	108^{ab}	(7.1)	53	(5.3)	59	(2.4)
BC_1(Tordo)S_1	79	(1.4)	72	(3.9)	66^{a}	(2.5)	100	(2.9)	107	(6.8)	95^{a}	(3.0)	106^{ab}	(7.1)	68	(5.3)	65	(2.4)
BC_1(Karamu)S_1	78	(1.4)	76	(3.9)	68^{a}	(2.5)	88	(2.9)	96	(6.8)	84^{c}	(3.0)	95^{b}	(7.1)	52	(5.3)	59	(2.4)
mean	77	(3.4)	74	(8.9)	66	(4.1)	91	(5.1)	104	(11.8)	91	(5.1)	104	(11.8)	57	(8.6)	61	(4.8)
Overall Mean	60	(2.5)	56	(6.7)	50	(4.4)	-		-		73	(5.1)	90	(12.3)	45	(9.1)	47	(4.2)
F-test[1]: Env.	**	[**]	**	[**]	**	[**]					**	[**]	(*)	[**]	**	[**]	**	[**]
Gen.	NS	[NS]	*	[*]	NS	[*]					NS	[**]	NS	[**]	NS	[NS]	NS	[NS]
GxE.	NS	[NS]	NS	[NS]	NS	[NS]					**	[**]	**	[**]	NS	[NS]	NS	[NS]

Least square means within each column within each environment which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;

* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

Table 2. Estimated times of occurrence of harvest ripeness and other stages of grain development of cross Tordo x Karamu (Cross 1), averaged across the two environments.

Generation	Harvest ripeness		Amylase maturity		GA-amylase maturity		Median embryo maturity		Embryo maturity		Dry weight maturity		Grain colour maturity	
Tordo	59	(1.0)	57^{ab}	(2.7)	55	(1.8)	96	(2.4)	119	(5.7)	43	(4.3)	48	(1.7)
Karamu	60	(1.0)	62^{a}	(2.7)	51	(2.0)	64	(2.4)	71	(5.7)	46	(3.7)	48	(1.7)
F_2	59	(1.0)	54^{abc}	(2.7)	52	(1.8)	73	(2.4)	95	(5.7)	43	(3.7)	46	(1.7)
F_3	58	(1.0)	48^{c}	(2.7)	45	(1.8)	65	(2.1)	78	(5.0)	43	(3.7)	45	(1.7)
BC_1(Tordo)S_1	61	(1.0)	52^{bc}	(2.7)	49	(1.8)	77	(2.1)	97	(5.0)	54	(3.7)	49	(1.7)
BC_1(Karamu)S_1	60	(1.0)	57^{ab}	(2.7)	48	(1.8)	64	(2.1)	77	(5.0)	39	(3.7)	45	(1.7)
Mean	60	(2.5)	56	(6.7)	50	(4.4)	73	(5.1)	90	(12.3)	45	(9.1)	47	(4.2)
Significance of generation effect[1]:	NS	[NS]	*	[*]	NS	[*]	NS	[**]	NS	[**]	NS	[NS]	NS	[NS]

Least square means within each column which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;

* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

Table 3 shows that α-amylase maturity, GA α-amylase maturity and harvest ripeness in cross 1 are different stages of development. Harvest ripeness also differs from grain coat maturity and dry weight maturity. The two variables which were not significantly different from each other are grain coat maturity and dry weight maturity.

Table 3. The tests for the difference between maturity variables and the correlation coefficients for some pairs of variables in cross 1.

Variable	GA amylase maturity	Harvest ripeness	Grain colour maturity	Dry weight maturity
Amylase maturity[1]	4.10 **	3.81 **		
	34	35		
	0.94 **	0.94 **		
GA amylase maturity		10.30 **		
		34		
		0.95 **		
Harvest ripeness			12.51 **	8.05 **
			35	34
			0.95 **	0.80 **
Grain colour maturity				1.22 NS
				34
				0.82 **

1 : Values in the first row are t-values for the paired t-test between the two variables; the values in the second row are the numbers of samples in the paired t-test and in computing the correlation coefficients ;
the values in the third row are the correlation coefficients.
** : significant values of t or correlation coefficients at the 1 % probability level.
NS : no significance difference between the means or non significant correlation coefficients.

I.3) Cross 2's Results

Changes in grain moisture content of the six generations of the wheat cross 2, Tordo x Gabo (GA insensitivity x white, non-dormant), in the warm and the cool ripening environments are presented in Figures A.3 and A.4 respectively. Harvest ripeness and times of occurrence of other maturity characters in this cross are presented in Table 4.

Table 4. Estimated times of occurrence of harvest ripeness and other stages of grain development of the six generations of wheat cross Tordo x Gabo (cross 2) grown in the two environments (in days after anthesis).

Generation	Harvest ripeness		Amylase maturity		GA-amylase maturity		Median embryo maturity		Embryo maturity		Dry weight maturity		Grain colour maturity	
						WARM ENVIRONMENT								
Tordo	41	(4.2)	46	(5.4)	44	(7.2)	63	(14.3)	65	(21.3)	31	(6.4)	30^{cd}	(2.9)
Gabo	50	(4.2)	50	(5.4)	48	(7.2)	43	(14.3)	75	(21.3)	26	(6.4)	42^{a}	(2.9)
F_2	40	(4.2)	56	(6.8)	37	(7.2)	52	(11.2)	77	(16.7)	29	(6.4)	39^{ab}	(2.9)
F_3	39	(4.2)	49	(5.4)	43	(7.2)	44	(11.2)	74	(16.7)	27	(6.4)	33^{bc}	(2.9)
$BC_1(Tordo)S_1$	41	(4.2)	45	(5.4)	54	(9.1)	53	(11.2)	77	(16.7)	32	(6.4)	26^{d}	(2.9)
$BC_1(Gabo)S_1$	40	(4.2)	43	(5.4)	47	(7.2)	36	(11.2)	52	(16.7)	28	(6.4)	29^{cd}	(2.9)
Mean	42	(6.3)	48	(6.6)	45	(8.2)	48	(6.5)	70	(15.7)	29	(3.8)	33	(4.5)
						COOL ENVIRONMENT								
Tordo	84	(4.2)	61	(5.4)	59	(7.2)	98^{b}	(14.2)	108	(21.2)	67	(6.4)	69^{a}	(2.9)
Gabo	80	(4.2)	64	(5.4)	80	(7.2)	124^{ab}	(11.2)	147	(16.7)	55	(6.4)	68^{a}	(2.9)
F_2	87	(4.2)	80	(5.4)	65	(7.2)	109^{ab}	(11.2)	148	(16.7)	53	(6.4)	72^{a}	(2.9)
F_3	83	(4.2)	81	(5.4)	59	(7.2)	101^{b}	(11.2)	134	(16.7)	50	(6.4)	68^{a}	(2.9)
$BC_1(Tordo)S_1$	81	(4.2)	72	(5.4)	60	(7.2)	130^{a}	(11.2)	171	(16.7)	67	(6.4)	54^{b}	(2.9)
$BC_1(Gabo)S_1$	80	(4.2)	78	(5.4)	46	(7.2)	111^{ab}	(11.2)	140	(16.7)	48	(6.4)	61^{b}	(2.9)
Mean	83	(8.0)	73	(11.1)	62	(15.4)	112	(26.0)	141	(37.0)	57	(15.3)	65	(5.4)
Overall Mean	62	(7.2)	60	(9.3)	54	(12.5)	80	(19.4)	106	(29.0)	43	(11.1)	49	(5.0)
F-test[1]:Env.	**	[**]	**	[**]	*	[**]	**	[**]	**	[**]	*	[**]	**	[**]
Gen.	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	*	[**]
G x E	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]

Least square means within each column within each environment which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;

* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

As in cross 1, the cool environment significantly delayed time to harvest ripeness as well as all other developmental stages of the wheat grain. Mean times to harvest ripeness, median embryo maturity, embryo maturity, dry weight maturity and grain colour maturity in the cool environment were approximately double those in the warm environment.

Table 5 shows the mean values of harvest ripeness and all other maturity characters of the six generations of wheat in this cross when averaged over the two ripening environments. The F-test results for combined analysis of variance showed a significant generation effect for grain colour maturity only ($P < 0.05$, Table 5).

Table 5. Estimated times of occurence of harvest ripeness and other stages of grain development of cross Tordo x Gabo (Cross 2), averaged across two environments.

Generation	Harvest ripeness		Amylase maturity		GA-amylase maturity		Median embryo maturity		Embryo maturity		Dry weight maturity		Grain colour maturity	
Tordo	63	(2.9)	53	(3.8)	52	(5.1)	80	(10.1)	87	(15.0)	49	(4.5)	50^{bc}	(2.0)
Gabo	65	(2.9)	57	(3.8)	64	(5.1)	83	(9.1)	111	(13.6)	41	(4.5)	55^{a}	(2.0)
F_2	64	(2.9)	68	(3.8)	51	(5.1)	81	(7.9)	113	(11.8)	41	(4.5)	55^{a}	(2.0)
F_3	61	(2.9)	65	(4.3)	51	(5.1)	73	(7.9)	104	(11.8)	39	(4.5)	50^{b}	(2.0)
BC_1(Tordo)S_1	61	(2.9)	58	(3.8)	57	(5.8)	92	(7.9)	124	(11.8)	50	(4.5)	40^{d}	(2.0)
BC_1(Gabo)S_1	60	(2.9)	61	(3.8)	47	(5.1)	74	(7.9)	96	(11.8)	38	(4.5)	45^{cd}	(2.0)
Mean	62	(7.2)	60	(9.3)	54	(12.5)	81	(19.4)	106	(29.0)	43	(11.1)	49	(5.0)
Significant of generation effect[1]:	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	NS	[NS]	*	[**]

Least square means within each column which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; * : significant at the 5 % probability level.

Values in parentheses are the standard errors of the estimates.

Comparison between variables to test whether they occurred at the same point of time or not were carried out using paired t-tests. The results are presented in Table 6. Only six pairs of variable combinations were tested.

Table 6 showed that amylase maturity and harvest ripeness occurred at the same point of time. This cross's results are different from cross 1's result in that the timing of dry weight maturity and grain colour maturity of this cross are significantly different.

Table 6. The tests for the difference between maturity variables and the correlation coefficients for some pairs of variables in cross 2.

Variable	GA amylase maturity	Harvest ripeness	Grain colour maturity	Dry weight maturity
Amylase maturity	2.60 * 33 0.35 *	0.83 NS 34 0.70 **		
GA amylase maturity		2.94 ** 34 0.51 **		
Harvest ripeness			7.12 ** 35 0.86 **	7.71 ** 35 0.72 **
Grain colour maturity				2.78 ** 35 0.70 **

1 : Values in the first row are t-values for paired t-test between the two variables; the values in the second row are the numbers of samples in the paired t-test and in computing the correlation coefficients ; the values in the third row are the correlation coefficients.
** : significant values of t or correlation coefficients at the 1 % probability level.
* : significant values of t or correlation coefficients at the 5 % probability level.
NS : not significance difference between the means or not significant correlation coefficients.

I.4) Cross 3's Results

Changes in grain moisture content of the six generations of wheat cross 3, Tordo x Sonora 64 A (GA insensitive x red, non-dormant), in the warm and in the cool ripening environments are presented in Figures A.5 and A.6, respectively. The estimated times of occurrence of nine events related with maturity and ripening of the six generations of wheat cross 3 are presented in Table 7.

As in the first two crosses the cool environment delayed harvest ripeness and all other developmental stages significantly. Differences among generation means when averaged over the two environments were detected for GA amylase maturity, median germination and for germination maturity (Table 8). GA amylase maturities of the two parental cultivars were not significantly different, but the F_2 generation had a significantly more rapid GA amylase maturity compared to the two parents. Median germination also showed a significant generation x environment interaction. In both environments Tordo had higher mean values of median germination than Sonora 64A. The two selfed backcrosses were significantly different from the recurrent parents in the warm environment but these differences disappeared in the cool environment.

Median embryo maturity and embryo maturity showed significant generation x environment interactions. In the warm environment Tordo had a later median embryo maturity and embryo maturity than Sonora 64A. But in the cool environment median embryo maturity of these two cultivars were not different and Sonora 64A had later embryo maturity compared to Tordo.

The sequence of developmental stages in this cross was similar to those of the earlier two crosses i.e.- dry weight maturity and grain colour maturity were the two earliest events followed by amylase maturity and GA amylase maturity. Harvest ripeness came after amylase maturities and was followed by median embryo maturity, median germination, embryo maturity (T90PG) and germination maturity (T90SG) respectively.

Table 7. Estimated times of occurrence of harvested ripeness and other stages of grain development of the six generations of wheat cross Tordo x Sonora 64A (cross 3) grown in the two environments (in days after anthesis).

Generation	Harvest ripeness	Amylase maturity	GA-amylase maturity	Median germination	Germination maturity	Median embryo maturity	Embryo maturity	Dry weight maturity	Grain colour maturity
				WARM ENVIRONMENT					
Tordo	42 (1.9)	48 (5.9)	54^{a} (10.7)	83^{a} (3.2)	93^{a} (6.5)	76^{a} (4.1)	90^{a} (5.7)	27 (4.7)	35 (4.2)
Sonora 64A	42 (1.9)	38 (4.6)	40^{a} (5.8)	38^{d} (4.0)	44^{c} (8.2)	38^{cd} (5.9)	36^{c} (8.2)	31 (4.7)	32 (4.2)
F_2	38 (1.9)	35 (4.6)	25^{b} (5.8)	52^{c} (3.2)	65^{b} (6.5)	46^{bc} (3.2)	43^{c} (4.4)	30 (4.7)	33 (5.3)
F_3	39 (1.9)	31 (4.6)	39^{ab} (5.8)	53^{c} (3.2)	65^{b} (6.5)	37^{d} (3.2)	51^{c} (4.4)	30 (4.7)	46 (4.2)
BC_1(Tordo)S_1	41 (1.9)	37 (5.9)	47^{a} (7.4)	67^{b} (3.2)	93^{a} (6.5)	53^{b} (3.2)	66^{b} (4.4)	28 (4.7)	28 (4.2)
BC_1(Sonora)S_1	39 (1.9)	43 (4.6)	45^{a} (5.8)	48^{c} (3.2)	60^{bc} (6.5)	37^{d} (4.1)	42^{c} (5.7)	27 (4.7)	28 (4.2)
Mean	40 (3.0)	39 (8.8)	42 (6.9)	57 (4.7)	70 (8.0)	48 (7.3)	55 (10.1)	29 (3.8)	34 (7.9)
				COOL ENVIRONMENT					
Tordo	78 (1.9)	72 (4.6)	77 (5.8)	118^{a} (3.2)	141^{ab} (6.5)	104^{a} (3.2)	117^{c} (4.4)	59 (4.7)	53 (4.2)
Sonora 64A	80 (1.9)	64 (4.6)	74 (5.8)	99^{b} (3.2)	116^{c} (6.5)	101^{ab} (3.2)	135^{a} (4.4)	56 (4.7)	52 (4.2)
F_2	78 (1.9)	64 (4.6)	59 (5.8)	104^{b} (3.2)	122^{c} (6.5)	102^{ab} (3.2)	130^{ab} (4.4)	68 (4.7)	61 (4.2)
F_3	80 (1.9)	66 (4.6)	67 (5.8)	104^{b} (3.2)	126^{bc} (6.5)	96^{bc} (3.2)	119^{bc} (4.4)	66 (4.7)	60 (4.2)
BC_1(Tordo)S_1	79 (1.9)	79 (4.6)	62 (5.8)	115^{a} (3.2)	152^{a} (6.5)	99^{ab} (3.2)	136^{a} (4.4)	65 (4.7)	61 (4.2)
BC_1(Sonora)S_1	80 (1.9)	72 (4.6)	72 (5.8)	103^{b} (3.2)	126^{abc} (6.5)	90^{c} (3.2)	119^{bc} (4.4)	62 (4.7)	60 (4.2)
Mean	79 (3.7)	70 (7.4)	68 (11.8)	107 (6.1)	130 (13.4)	99 (4.0)	126 (5.7)	63 (10.8)	58 (6.6)
Overall Mean	60 (3.3)	54 (8.1)	55 (10.1)	82 (5.5)	100 (11.2)	73 (5.5)	90 (7.7)	46 (8.1)	46 (7.3)
F-test[1]:Env.	** [**]	** [**]	** [**]	** [**]	** [**]	** [**]	** [**]	** [**]	** [**]
Gen.	NS [NS]	NS [(*)]	(*) [*]	* [**]	** [**]	NS [**]	NS [**]	NS [NS]	NS [NS]
GxE.	NS [NS]	NS [NS]	NS [NS]	* [*]	NS [NS]	** [**]	** [**]	NS [NS]	NS [NS]

Least square means within each column within each environment which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;

* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

Table 8. Estimated times of occurence of harvest ripeness and other stages of grain development of cross Tordo x Sonora 64A (Cross 3) averaged across two environments.

Generation	Harvest ripeness	Amylase maturity	GA-amylase maturity	Median germination	Germination maturity	Median embryo maturity	Embryo maturity	Dry weight maturity	Grain colour maturity
Tordo	60 (1.4)	60 (3.8)	65^{a} (6.1)	101^{a} (2.2)	117^{a} (4.6)	90 (2.6)	103 (3.6)	43 (3.3)	44 (3.0)
Sonora 64A	61 (1.4)	49 (3.3)	57^{a} (4.1)	68^{d} (2.6)	80^{c} (5.2)	70 (3.3)	85 (4.7)	44 (3.3)	42 (3.0)
F_2	58 (1.4)	49 (3.3)	42^{b} (4.1)	78^{c} (2.2)	93^{b} (4.6)	74 (2.2)	86 (3.1)	49 (3.3)	47 (3.4)
F_3	59 (1.4)	49 (3.3)	53^{a} (4.1)	78^{c} (2.2)	95^{b} (4.6)	67 (2.2)	85 (3.1)	48 (3.3)	53 (3.0)
BC_1(Tordo)S_1	60 (1.4)	58 (3.8)	54^{a} (4.7)	91^{b} (2.2)	122^{a} (4.6)	76 (2.2)	101 (3.1)	47 (3.3)	44 (3.0)
BC_1(Sonora)S_1	59 (1.4)	58 (3.3)	58^{a} (4.1)	76^{c} (2.2)	93^{b} (4.6)	64 (2.6)	80 (3.6)	44 (3.3)	44 (3.0)
Mean	60 (3.3)	54 (8.1)	55 (10.1)	82 (5.5)	100 (11.2)	74 (5.5)	90 (7.7)	46 (8.1)	46 (7.3)
Significant generation effect[1]:	NS [NS]	NS [(*)]	(*) [*]	* [**]	** [**]	NS [**]	NS [**]	NS [NS]	NS [NS]

Least square means within each column which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;
* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

The test for differences between maturity variables were carried out by paired t-tests. Six pairs of comparisons were tested. The results are presented in Table 9.

In cross 3, α-amylase maturity and GA amylase maturity were not significantly different, also grain colour maturity and dry weight maturity were alike (Table 9).

Table 9. The tests for the difference between maturity variables and the correlation coefficients for some pairs of variables in cross 3.

Variable	GA amylase maturity	Harvest ripeness	Grain colour maturity	Dry weight maturity
Amylase maturity	0.02 NS 32 0.75 **	3.67 ** 33 0.87 **		
GA amylase maturity		3.16 ** 32 0.84 **		
Harvest ripeness			7.37 ** 34 0.82 **	10.74 ** 35 0.92 **
Grain colour maturity				0.02 NS 34 0.81 **

1 : Values in the first row are t-values for paired t-test between the two variables; the values in the second row are the numbers of samples in the paired t-test and in computing the correlation coefficients; the values in the third row are the correlation coefficients.
** : significant values of t or correlation coefficients at the 1 % probability level.
NS : not significance difference between the means or not significant correlation coefficients.

I.5) Comparisons of Tordo's Maturities Characters Between Crosses

The times to harvest ripeness and other maturity characters of Tordo in the different crosses were compared by t-tests. The comparison were conducted for each environment and for the averaged means across the two environments. The t-values are presented in Table 10.

Table 10. The test of differences between the mean values of maturity variables of Tordo in different crosses.

Characters	Environment	Comparisons between crosses :	Mean Diff.[a]	T	Sig.[b]
Harvest ripeness	Warm	1 vs 2	0.0	0.000	ns
		1 vs 3	-1.0	-0.424	ns
		2 vs 3	-1.0	-0.217	ns
	Cool	1 vs 2	-8.0	-1.807	ns
		1 vs 3	-2.0	-0.847	ns
		2 vs 3	6.0	1.302	ns
	Pool	1 vs 2	-4.0	-1.304	ns
		1 vs 3	-1.0	-0.581	ns
		2 vs 3	3.0	0.932	ns
Amylase maturity	Warm	1 vs 2	-7.0	-1.051	ns
		1 vs 3	-9.0	-1.273	ns
		2 vs 3	-2.0	-0.250	ns
	Cool	1 vs 2	15.0	2.252	(*)
		1 vs 3	4.0	0.663	ns
		2 vs 3	-11.0	-1.551	ns
	Pool	1 vs 2	4.0	0.858	ns
		1 vs 3	-3.0	-0.644	ns
		2 vs 3	-7.0	-1.303	ns
GA amylase maturity	Warm	1 vs 2	-6.0	-0.787	ns
		1 vs 3	-16.0	-6.163	**
		2 vs 3	-10.0	-1.382	ns
	Cool	1 vs 2	12.0	1.574	ns
		1 vs 3	-6.0	-0.950	ns
		2 vs 3	-18.0	-1.947	ns
	Pool	1 vs 2	3.0	0.555	ns
		1 vs 3	-10.0	-1.572	ns
		2 vs 3	-13.0	-1.635	ns
Median embryo maturity	Warm	1 vs 2	35.0	6.170	**
		1 vs 3	5.0	0.669	ns
		2 vs 3	-30.0	-3.849	*
	Cool	1 vs 2	-3.0	-0.581	ns
		1 vs 3	-46.0	-6.426	**
		2 vs 3	-43.0	-5.556	**
	Pool	1 vs 2	16.0	6.661	**
		1 vs 3	-21.0	-4.047	**
		2 vs 3	-37.0	-8.042	**

Table 10. (continue)

Characters	Environment	Comparisons between crosses :	Mean Diff.[a]	T	Sig.[b]
Embryo maturity	Warm	1 vs 2	69.0	7.588	**
		1 vs 3	44.0	4.130	*
		2 vs 3	-25.0	-4.276	*
	Cool	1 vs 2	-4.0	-0.556	ns
		1 vs 3	-13.0	-1.556	ns
		2 vs 3	-9.0	-1.973	ns
	Pool	1 vs 2	32.0	4.220	**
		1 vs 3	16.0	2.373	*
		2 vs 3	-16.0	-2.597	*
Dry weight maturity	Warm	1 vs 2	-5.0	-0.540	ns
		1 vs 3	-1.0	-0.122	ns
		2 vs 3	4.0	0.504	ns
	Cool	1 vs 2	-7.0	-0.842	ns
		1 vs 3	1.0	0.141	ns
		2 vs 3	8.0	1.008	ns
	Pool	1 vs 2	-6.0	-0.964	ns
		1 vs 3	0.0	0.000	ns
		2 vs 3	6.0	1.075	ns
Grain colour maturity	Warm	1 vs 2	4.0	1.063	ns
		1 vs 3	-1.0	-0.207	ns
		2 vs 3	-5.0	-0.980	ns
	Cool	1 vs 2	-8.0	-2.125	ns
		1 vs 3	8.0	1.654	ns
		2 vs 3	16.0	3.135	*
	Pool	1 vs 2	-2.0	-0.762	ns
		1 vs 3	4.0	1.160	ns
		2 vs 3	6.0	1.664	ns
Median germination	Cool	1 vs 3	6.0	1.389	ns
Germination maturity	Cool	1 VS 3	-27.0	-2.870	*

a : Mean difference.
b : Significant symbols , ns = not significantly different at the 10 % probability level, (*) = significantly different at the 10 % probability level, * = significantly different at the 5 % probability level and; ** = significantly different at the 1 % probability level.

Table 10 shows that median embryo maturity and embryo maturity of Tordo in different crosses were significantly different in many comparisons. Harvest ripeness, amylase maturity, GA amylase maturity, dry weight maturity and grain colour maturity were generally not significantly different between crosses.

II) GERMINATION PERCENTAGES AT HARVEST RIPENESS

II.1) Cross 1's Results

Changes in the standard germination percentages of the six generations of wheat cross 1 ripening in the warm and in the cool environments are presented in Figures A.7 and A.8 respectively. Also the changes in the potential germination of the six generations in the warm and cool environments are presented in Figures A.9 and A.10, respectively. Germination percentages of the grains at harvest ripeness for the two germination tests along with the percentage dormancy of this cross are presented in Table 11. The dormancy percentage were computed according to the formula given earlier (section VII.1.4, Chapter 3). The means of the six generations averaged across the two environments are presented in Table 12.

Table 11. Percentage standard germination, potential germination and dormancy at harvest ripeness of the six generations of wheat cross Tordo x Karamu (cross 1) grown in the two environments.

Environment	Generation	Standard germination at HR		Potential germination at HR		Dormancy at HR
Warm	Tordo	0^{c}	(2.3)	0^{c}	(9.4)	-
	Karamu	2^{c}	(2.3)	41^{ab}	(9.4)	95
	F_2	11^{b}	(2.3)	23^{bc}	(12.9)	52
	F_3	23^{a}	(2.3)	54^{a}	(7.4)	57
	BC_1(Tordo)S_1	4^{c}	(2.3)	20^{c}	(7.4)	80
	BC_1(Karamu)S_1	3^{c}	(2.3)	47^{ab}	(7.4)	94
Mean		7	(4.0)	31	(13.5)	77
Cool	Tordo	0^{b}	(1.8)	2	(7.4)	100
	Karamu	0^{b}	(1.8)	3	(7.4)	100
	F_2	0^{b}	(1.8)	8	(7.4)	100
	F_3	7^{a}	(1.8)	13	(7.4)	46
	BC_1(Tordo)S_1	1^{b}	(1.8)	0	(7.4)	-
	BC_1(Karamu)S_1	9^{a}	(1.8)	35	(7.4)	74
Mean		3	(3.2)	10	(12.3)	70
Mean		5	(3.6)	21	(12.8)	76
F-test results[1]:	Env.	NS		*		
	Gen.	NS		NS		
	G x E.	**		NS		

Least square means within each column within each environment which have a common letter are not significantly different by t-test at the 10 % probability level.
1 NS : Non significant; * : significant at the 5 % probability level; ** : significant at the 1 % probability level.
Values in parentheses are the standard errors of the least square means.

The standard germination at harvest ripeness showed a highly significant generation x environment interaction. In both environments the two parental cultivars had the same level of standard germination. The standard germination at harvest ripeness of the F_2 and F_3 generations in the warm ripening environments were significantly higher than the two parents, but in the cool ripening environment only the F_3 generation had a higher percent standard germination than the two parents.

The potential germination at harvest ripeness of grains developed in the cool environment was significantly lower than that of grains developed in the warm environment. There were significant differences

for potential germination at harvest ripeness among generations in the warm ripening environment ($P < 0.05$). Karamu had a significantly higher potential germination at harvest ripeness compared to Tordo which had zero potential germination.

The dormancy percentage computed from the mean values of the two germination tests appeared to be very high for both parents. For F_2 in the warm environment and F_2 and F_3 in the cool environment the dormancy level was only about half of that in the parental cultivars.

Table 12. Standard germination, potential germination and dormancy at harvest ripeness of the six generations of wheat cross Tordo x Karamu (cross 1), averaged across two environments.

Generation	Standard germination at HR		Potential germination at HR		Dormancy at HR
Tordo	0	(1.5)	1	(6.0)	100
Karamu	1	(1.5)	22	(6.0)	95
F_2	6	(1.5)	15	(7.9)	60
F_3	13	(1.5)	33	(5.2)	61
BC_1 (Tordo) S_1	2	(1.5)	12	(5.2)	83
BC_1 (Karamu) S_1	6	(1.5)	41	(5.2)	85
Mean	5	(3.6)	21	(12.8)	76
Significance of generation effects[1] :	NS		NS		

1 NS : Non significant.
Values in parentheses are the standard errors of the least square means.

II.2) Cross 2's Results

Changes in the standard germination percentages of the six generations of wheat cross 2 (Tordo x Gabo) developing in the warm and the cool environments are presented in Figures A.11 and A.12 respectively. The changes in potential germination of the six generations of this cross in the warm and cool environments are presented in Figure A.13 and A.14.

Table 13 shows the standard and potential germination at harvest ripeness. and the percentage dormancy of the six generations of wheat cross 2 ripening in the two environments. Mean values averaged across the two environments are presented in Table 14. The potential germination at harvest ripeness of grain which had developed in the cool environment was significantly lower than that of grains developed in the warm environment (Table 13). There was highly significant generation x environment interaction for potential germination at harvest ripeness. Under the warm ripening environment, Gabo showed significantly higher potential germination at harvest ripeness than did Tordo. Under the cool ripening environment the two cultivars did not differ in potential germination at harvest ripeness.

Table 13. Percentage standard germination, potential germination and dormancy at harvest ripeness of the six generations of wheat cross Tordo x Gabo (Cross 2) grown in the two environments.

Environment	Generation	Standard germination at HR		Potential germination at HR		Dormancy at HR
Warm	Tordo	1	(8.1)	0^{d}	(8.6)	-
	Gabo	39	(8.1)	63^{a}	(8.6)	38
	F_2	17	(8.1)	27^{bc}	(6.7)	37
	F_3	14	(8.1)	41^{b}	(6.7)	66
	BC_1(Tordo)S_1	4	(8.1)	21^{c}	(6.7)	81
	BC_1(Gabo)S_1	18	(8.1)	65^{a}	(6.7)	72
Mean		16	(16.4)	36	(14.0)	56
Cool	Tordo	5	(14.9)	6^{bc}	(8.6)	17
	Gabo	7	(8.1)	2^{c}	(6.8)	0
	F_2	18	(8.1)	25^{a}	(6.8)	28
	F_3	8	(8.1)	24^{ab}	(6.8)	67
	BC_1(Tordo)S_1	8	(8.1)	14^{abc}	(6.8)	43
	BC_1(Gabo)S_1	6	(10.3)	10^{abc}	(6.8)	40
Mean		9	(9.5)	13	(9.3)	31
Mean over two env.		12	(14.0)	25	(11.7)	52
F-test results[1] :	Env.	NS		(*)		
	Gen.	NS		NS		
	G x E.	NS		**		

Least square means within each column within each environment which have a common letter are not significantly different by t-test at 10 % probability level.
1 NS : Non significant;(*) : significant at the 10 % probability level; ** : significant at the 1 % probability level.
Values in parentheses are the standard errors of the least square means.

Table 14. Standard germination and potential germination at harvest ripeness of the six generations of wheat cross Tordo x Gabo (Cross 2), averaged across two environments.

Generation	Standard germination at HR		Potential germination at HR		Dormancy at HR
Tordo	3	(8.5)	2	(6.1)	-
Gabo	23	(5.7)	32	(5.5)	28
F_2	18	(5.7)	26	(4.8)	31
F_3	11	(5.7)	33	(4.8)	67
BC_1(Tordo)S_1	5	(5.7)	17	(4.8)	71
BC_1(Gabo)S_1	12	(6.5)	38	(4.8)	68
Mean	12	(14.0)	25	(11.7)	52
Significance of generation effects[1] :	NS		NS		

1 NS : Non significant.
Values in parentheses are the standard errors of the least square means.

II.3) Cross 3's Results

Changes in the percentage standard germination at harvest ripeness of the six generations of wheat cross 3 (Tordo x Sonora 64A) developed in the warm and cool ripening environment are presented in Figures A.15 and A.16 respectively. Changes in potential germination at harvest ripeness of the six generations of this cross developed in the warm ripening environment and in the cool ripening environment are presented in Figures A.17 and A.18. The germination percentages at harvest ripeness and per cent dormancy of the six generations of this cross developed in the two ripening environments are presented in Table 15. The means of the six generations are presented in Table 16.

No significant environmental effect or generation effects were detected for standard germination at harvest ripeness. However grains developed in the cool ripening environment had significantly lower percentages of potential germination at harvest ripeness ($P<0.10$). In the warm ripening environment Tordo had significantly

lower potential germination at harvest ripeness compared to Sonora 64A, but in the cool ripening environment both cultivars had low potential germination and did not differ from each other.

Table 15. Percentage standard germination, potential germination and dormancy at harvest ripeness of the six generations of wheat cross Tordo x Sonora 64A (cross 3) grown in the two environments.

Environment	Generation	Standard germination at HR		Potential germination at HR		Dormancy at HR
Warm	Tordo	0	(7.9)	0^{b}	(11.6)	-
	Sonora 64A	49	(10.0)	87^{a}	(16.8)	44
	F_2	10	(7.9)	62^{a}	(9.0)	84
	F_3	11	(7.9)	62^{a}	(9.0)	82
	BC_1(Tordo)S_1	12	(7.9)	14^{b}	(9.0)	14
	BC_1(Sonora)S_1	15	(7.9)	65^{a}	(11.6)	77
Mean		16	(18.7)	48	(21.9)	67
Cool	Tordo	2	(7.9)	1^{b}	(9.0)	-
	Sonora 64A	8	(7.9)	19^{ab}	(9.0)	58
	F_2	5	(7.9)	13^{ab}	(9.0)	62
	F_3	7	(7.9)	16^{ab}	(9.0)	56
	BC_1(Tordo)S_1	9	(7.9)	23^{ab}	(9.0)	61
	BC_1(Sonora)S_1	13	(7.9)	33^{a}	(9.0)	61
Mean		8	(6.4)	18	(10.1)	56
Mean over two env.		12	(13.7)	33	(15.6)	64
F-test results[1] :	Env.	NS		(*)		
	Gen.	NS		NS		
	G x E.	NS		**		

Least square means within each column within each environment which have a common letter are not significantly different by t-test at 10 % probability level.

1 NS : Non significant;(*) : significant at the 10 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the least square means.

TRANSFOMATION OF GERMINATION DATA.

The data for percentage germinations (standard germination and potential germination) in these experiments were not transformed to arcsine, as done in some reports on germination experiments. The arcsine transformation is applicable to binomial data expressed as decimal fractions or percentages, and is especially recommended when the percentages cover a wide range of values (Steel and Torrie, 1980). The unit of arcsine transformation is degrees or radians. Bartlett (1947) suggested that the transformed data should have the following characters:-

"(a) The variance of the transformed variate should be unaffected by changes in the mean level.

(b) The transformed variate should be normally distributed.

(c) The transformed scale should be one for which arithmatic average is an efficient estimate of the true mean level for any particular group of measurements.

(d) The transformed scale should be one for which real effects are linear and additive."

Thus, transformation may be used to change the data to fit the assumptions for analysis of variance. The assumptions have been described by Cochran (1947) as follows:

(1) The treatment effects and the block effects must be additive.

(2) The experimental errors must be independent.

(3) The experimental errors must have a common variance.

(4) The experimental errors should be normally distributed.

In the germination tests , the state of seeds under the test may be one of two kinds,i.e. germinable or not germinable, suggesting that the data may have a binomial distribution. The expectation of the grain germinability can be calculated by the formular $(P + Q)^n$. Where P is the probability that the grain will germinate, and Q is the probability that the grain will not germinate. The number of seeds in the test equal to n. However, P and Q in the present experiments are not constants for all generations because they are determined by genetic and environmental effects sampled in the experiment. Thus the germination in an experiment of this kind can be considered to be normally distributed rather than binomial data. This is the attitude adopted in the present study.

In genetic study the scale used to represent the degree of expression of a character can affect the apparent occurrence, direction and degree of dominance and epistasis (Mather and Jinks, 1971). Further, by changing the scale the relative magnitude of genotype x environment effects will change in such a way that they may be reduced or almost neligible. Therefore, the choice of scale can be crucial to such studies.

In biometrical genetics, some people suggested that a scale should be chosen so as to remove as far as possible the effects of non allelic interactions and genotype x environment interactions, allowing dominance to take its own value on the scale so reached (Mather and Jinks, 1971).

Mather and Jinks (1971) have pointed out that "discovery of an empirically satisfactory scale cannot of itself be used to justify theoretical conclusions concerning the physiology of gene action". So without the empirical knowledge of what the appropriate scale for the character should be, the transformation will not give a clue to what type of gene effects are important. Therefore, it may be better to use natural scale as far as possible, so that the results are not predetermined by scale choice. Therefore, considering this point together with the earlier discussion on the variability of binomial P and Q, it has been decided to analyse germination data in natural scale.

Table 16. Percentage standard germination, potential germination and dormancy at harvest ripeness of the six generations of wheat cross Tordo x Sonora 64A (cross 3), averaged across two environments (in percent).

Generation	Standard germination at HR		Potential germination at HR		Dormancy at HR
Tordo	1	(5.6)	0	(7.4)	-
Sonora 64A	29	(6.4)	53	(9.5)	45
F_2	7	(5.6)	38	(6.4)	82
F_3	9	(5.6)	39	(6.4)	77
BC_1(Tordo)S_1	10	(5.6)	18	(6.4)	44
BC_1(Sonora)S_1	14	(5.6)	49	(7.4)	71
Mean	12	(13.7)	33	(15.6)	64
Significance of generation effects[1] :	NS		NS		

NS : non significant at the 10 % probability level.
Values in parentheses are the standard errors of the least square means.

II.4) Comparison Among Crosses

The performances of the parental cultivars in the two ripening environments have been compared. Tordo developed in the two ripening environments consistently showed low germination percentages. Karamu ripening in the warm environment showed a moderate level of potential germination (41%) but had a low level of standard germination at harvest ripeness. When ripening in the cool environment, this cultivar had a low level of standard germination and potential germination at harvest ripeness. The two sprouting susceptible cultivars, Gabo and Sonora 64A showed moderate levels of standard germination at harvest ripeness and high levels of potential germination at harvest ripeness. But both cultivars ripening in the cool environment exhibited low levels of germination. The effect of dormancy breaking treatments was more effective with grain ripening in the warm environment, and did not appear to be correlated to sprouting susceptibility.

III) GRAIN DRY WEIGHT AT HARVEST RIPENESS AND MAXIMUM GRAIN DRY WEIGHT

III.1) Cross 1's Results

Changes in grain dry weights during grain development and maturity for the six generations of wheat from cross Tordo x Karamu grown in the warm and the cool environments are presented in Figures A.19 and A.20 respectively. Grain dry weight at harvest ripeness and maximum grain dry weight (mg/grain) of the six generations of wheat in cross 1 ripening in the two environments are presented in Table 17. The mean values, averaged over the two environments are presented in Table 18.

Table 17. Grain dry weight at harvest ripeness and maximum grain dry weight (mg/grain) of six generations of wheat cross 1 (Tordo x Karamu) grown in the two environments.

Environment	Generation	Grain dry weight at HR.		Maximum grain dry weight	
Warm	Tordo	41.5^{b}	(1.7)	41.5^{c}	(1.7)
	Karamu	43.5^{ab}	(1.3)	45.7^{a}	(1.3)
	F_2	41.8^{b}	(1.3)	47.2^{a}	(1.3)
	F_3	45.5^{a}	(1.3)	47.5^{a}	(1.3)
	BC_1(Tordo)S_1	42.8^{ab}	(1.3)	47.4^{a}	(1.3)
	BC_1(Karamu)S_1	43.2^{ab}	(1.3)	43.5^{b}	(1.3)
Mean		43.0	(2.1)	45.4	(1.9)
Cool	Tordo	54.4^{abc}	(1.3)	56.8^{b}	(1.3)
	Karamu	55.2^{abc}	(1.3)	56.7^{b}	(1.3)
	F_2	55.8^{ab}	(1.3)	56.7^{b}	(1.3)
	F_3	52.4^{c}	(1.3)	53.6^{b}	(1.3)
	BC_1(Tordo)S_1	57.9^{a}	(1.3)	62.0^{a}	(1.3)
	BC_1(Karamu)S_1	53.5^{bc}	(1.3)	54.4^{b}	(1.3)
Mean		54.9	(2.1)	56.7	(2.6)
Mean over two env.		49.0	(2.3)	51.1	(2.3)
F-test results[1]:	Env.	**		**	
	Gen.	NS		NS	
	G x E.	(*)		*	

Least square means within each column within each environment which have a common letter are not significantly different by t-test at 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level; * : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the least square means.

Table 18. Grain dry weight at harvest ripeness and maximum grain dry weight (in mg/grain) of six generations of wheat cross Tordo x Karamu (Cross 1) averaged across two environments.

Generation	Grain dry weight at HR		Maximum grain dry weight	
Tordo	48.0	(1.1)	49.2	(1.1)
Karamu	49.4	(0.9)	51.2	(0.9)
F_2	48.7	(0.9)	51.9	(0.9)
F_3	48.9	(0.9)	50.5	(0.9)
BC_1(Tordo)S_1	50.3	(0.9)	54.7	(0.9)
BC_1(Karamu)S_1	48.3	(0.9)	48.9	(0.9)
Mean	48.9	(2.3)	51.1	(2.3)
Significance of generation effect[1]:	NS		NS	

1 NS : non significant at the 10 % probability level.
Values in parentheses are the standard errors of the least square means.

The cool environment significantly increased grain dry weight at harvest ripeness and maximum grain dry weight (Table 17). There were no significant generation effects for grain dry weight at harvest ripeness nor maximum grain dry weight. But the generation x environment interactions were significant for grain dry weight at harvest ripeness ($P < 0.10$) and for maximum grain dry weight ($P<0.05$). The grain dry weight of the F_3 generation ranked as the highest in the warm ripening environment, but in the cool ripening environment this generation had the lowest value. Karamu had a significantly higher maximum grain dry weight than Tordo in the warm ripening environment, but this difference disappeared in the cool environment.

III.2) Cross 2's Results

Changes in grain dry weight of the six generations of wheat cross 2 (Tordo x Gabo) developed in the warm environment and in the cool environment are presented in Figures A.21 and A.22 respectively. Grain dry weight at harvest ripeness (HRDW) and maximum grain dry weight (MAXDW) of the six generations of wheat in this cross are presented in Table 19. The mean values, averaged over the two environments, of the six generations of wheat in this cross are presented in Table 20.

Table 19. Grain dry weights at harvest ripeness and maximum grain dry weights of six generations of wheat cross 2 (Tordo x Gabo) grown in the two environments (mg/grain).

Environment	generation	Grain dry weight at HR		Maximum grain dry weight	
Warm	Tordo	45.9	(1.5)	47.7	(2.1)
	Gabo	45.7	(1.5)	46.1	(2.1)
	F_2	46.6	(1.5)	48.1	(2.1)
	F_3	45.2	(1.5)	46.2	(2.1)
	BC_1(Tordo)S_1	46.2	(1.5)	48.3	(2.1)
	BC_1(Gabo)S_1	44.8	(1.5)	45.8	(2.1)
Mean		45.7	(0.9)	47.0	(1.4)
Cool	Tordo	52.8	(1.5)	56.5	(2.1)
	Gabo	59.6	(1.5)	60.7	(2.1)
	F_2	55.1	(1.5)	55.8	(2.1)
	F_3	56.6	(1.5)	57.2	(2.1)
	BC_1(Tordo)S_1	54.7	(1.5)	59.4	(2.1)
	BC_1(Gabo)S_1	56.4	(1.5)	56.7	(2.1)
Mean		55.9	(3.6)	57.7	(5.0)
Mean over two env.		50.8	(2.6)	52.4	(3.7)
F-test results[1]:	Env.	**		**	
	Gen.	NS		NS	
	G x E.	NS		NS	

1 NS : Non significant; ** : significant at the 1 % probability level.
Values in parentheses are the standard errors of the least square means.

Table 20. Grain dry weight at harvest ripeness and maximum grain dry weight (mg/grain) of six generations of wheat cross Tordo X Gabo (Cross 2), averaged across two environments.

Generation	Grain dry weight at HR		Maximum grain dry weight	
Tordo	49.3	(1.1)	52.1	(1.5)
Gabo	52.7	(1.1)	53.4	(1.5)
F_2	50.8	(1.1)	52.0	(1.5)
F_3	50.9	(1.1)	51.7	(1.5)
BC_1 (Tordo) S_1	50.4	(1.1)	53.9	(1.5)
BC_1 (Gabo) S_1	50.6	(1.1)	51.2	(1.5)
Mean	50.8	(2.6)	52.4	(3.7)
Significance of generation effect[1] :	NS		NS	

NS : non significant difference at the 10 % probability level.
Values in parentheses are the standard errors of the least square means.

As in cross 1, the cool environment significantly increases both the grain dry weight at harvest ripeness and maximum grain dry weight. However this cross showed no significant differences among generations or significant generation x environment interactions.

III.3) Cross 3's Results

Changes in grain dry weight of the six generations of wheat cross 3 (Tordo x Sonora 64A) ripening in the warm environment and in the cool environment are presented in Figures A.23 and A.24 respectively. Grain dry weight at harvest ripeness and maximum grain dry weight of the six generations of wheat cross 3 are presented in Table 21. The mean values of these two variables averaged over the two environments are presented in Table 22.

Table 21. Grain dry weight at harvest ripeness and maximum grain dry weight (in mg/grain) of six generations of wheat in cross 3 grown in two environments.

Environment	Generation	Grain dry weigh at HR		Maximum grain dry weight	
Warm	Tordo	46.4[a]	(1.6)	46.9[a]	(1.7)
	Sonora 64 A	40.3[c]	(1.6)	41.6[bc]	(1.7)
	F_2	43.4[abc]	(1.6)	45.3[ab]	(1.7)
	F_3	44.3[ab]	(1.6)	46.0[a]	(1.7)
	BC_1(Tordo)S_1	42.6[bc]	(1.6)	43.7[abc]	(1.7)
	BC_1(Sonora)S_1	40.2[c]	(1.6)	41.2[c]	(1.7)
Mean		42.9	(2.5)	44.1	(2.5)
Cool	Tordo	58.4	(1.6)	60.2	(1.7)
	Sonora 64A	57.4	(1.6)	58.6	(1.7)
	F_2	58.1	(1.6)	61.8	(1.7)
	F_3	58.4	(1.6)	61.4	(1.7)
	BC_1(Tordo)S_1	55.4	(1.6)	58.9	(1.7)
	BC_1(Sonora)S_1	57.9	(1.6)	60.3	(1.7)
Mean		57.6	(2.9)	60.2	(3.2)
Mean		50.2	(2.7)	52.2	(2.9)
F-test results[1]:	Env.	**		**	
	Gen.	NS		NS	
	G x E.	NS		NS	

Least square means within each column within each environment which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; ** : significant at the 1 % probability level. Values in parentheses are the standard errors of the least square means.

Table 22. Grain dry weight at harvest ripeness and maximum grain dry weight (mg/grain) of six generations of wheat cross Tordo X Sonora 64A (Cross 3) averaged across two environments.

Generation	Grain dry weight at HR	Maximum grain dry weight
Tordo	52.4 (1.1)	53.5 (1.2)
Sonora 64A	48.8 (1.1)	50.1 (1.2)
F_2	50.8 (1.1)	53.5 (1.2)
F_3	51.3 (1.1)	53.7 (1.2)
BC_1(Tordo)S_1	49.0 (1.1)	51.3 (1.2)
BC_1(Sonora)S_1	49.0 (1.1)	50.8 (1.2)
Mean	50.2 (2.7)	52.2 (2.9)
Significance of generation effects[1]:	NS	NS

1 NS : not significant difference at the 10 % probability level. Values in parentheses are the standard errors of the least square means.

Differences in grain dry weight at harvest ripeness and maximum grain dry weight among generations were detected in only the warm environment. Tordo had heavier grain dry weight at harvest ripeness and had heavier maximum grain dry weight than Sonora 64A. F-test results for combined analyses of variance showed highly significant environmental effects. The cool environment significantly increased grain dry weights compared to those in the warm environment.

IV) α-AMYLASE CONTENTS IN THE GRAINS AT HARVEST RIPENESS AND EMBRYO MATURITY

IV.1) Cross 1's Results

Changes in base α-amylase level of the six generations of wheat cross 1 developed under the warm and the cool environments are presented in Figure A.25 and Figure A.26 respectively. Those for germinative α-amylase are presented in Figure A.27 and Figure A.28, and for GA α-amylase in Figure A.29 and Figure A.30. The levels of each types of α-amylase activity at harvest ripeness and at embryo maturity of the six generations of cross 1 wheat developed under warm and cool ripening environments are presented in Table 23. The mean values of the six variables averaged over the two environments are presented in Table 24.

Table 23. The levels of the three types of α-amylase activities at harvest ripeness and at embryo maturity of six generations of wheat in cross Tordo x Karamu (cross 1) grown in the two environments (in log. mEU/g).

Generation	Base α-amylase				Germinative α-amylase				GA3 α-amylase			
	at HR		at embryo maturity		at HR		at embryo maturity		at HR		at embryo maturity	
					WARM ENVIRONMENT							
Tordo	3.2490	(0.0919)	NA	(-)	3.3110^{b}	(0.2075)	NA	(-)	3.6347	(0.2385)	NA	(-)
Karamu	3.3339	(0.0919)	2.1693^{c}	(1.4720)	3.1617^{b}	(0.2075)	5.4721^{bc}	(1.1252)	4.6632	(0.2385)	5.6760^{cd}	(0.6881)
F_2	3.3314	(0.0919)	4.5822^{bc}	(1.4720)	3.9663^{a}	(0.2075)	5.4023^{bc}	(1.1252)	4.0899	(0.2385)	6.7774^{bc}	(0.6881)
F_3	3.3795	(0.0919)	3.1139^{bc}	(1.1597)	4.2165^{a}	(0.2075)	4.6084^{c}	(0.8865)	4.5225	(0.2385)	4.9537^{d}	(0.5421)
BC_1(Tordo)S_1	3.4116	(0.0919)	5.8829^{b}	(1.1597)	4.1292^{a}	(0.2075)	7.0067^{b}	(0.8865)	4.5261	(0.2385)	7.4240^{b}	(0.5421)
BC_1(Karamu)S_1	3.1879	(0.0919)	2.9085^{c}	(1.1597)	3.4387^{b}	(0.2075)	5.4877^{bc}	(0.8865)	4.9700	(0.2385)	6.3915^{bc}	(0.5421)
Mean	3.3155	(0.1746)	3.7314	(3.1143)	3.7039	(0.4123)	5.5954	(2.2648)	4.4011	(0.5215)	6.2445	(0.8477)
					COOL ENVIRONMENT							
Tordo	3.4304	(0.0919)	2.7471	(1.1597)	2.7532	(0.2075)	4.4757	(0.8865)	3.1908	(0.2385)	4.6611	(0.5421)
Karamu	3.1080	(0.0919)	2.8251	(1.1597)	2.9564	(0.2075)	4.0486	(0.8865)	3.1058	(0.2385)	3.8818	(0.5421)
F_2	3.3794	(0.0919)	3.0266	(1.1597)	2.8211	(0.2075)	4.6921	(0.8865)	3.4386	(0.2385)	5.7192	(0.5421)
F_3	3.4704	(0.0919)	2.9431	(1.1597)	3.4108	(0.2075)	4.9147	(0.8865)	3.7753	(0.2385)	4.9527	(0.5421)
BC_1(Tordo)S_1	3.2949	(0.0919)	2.8696	(1.1597)	3.1217	(0.2075)	3.3801	(0.8865)	3.2449	(0.2385)	3.8487	(0.5421)
BC_1(Karamu)S_1	3.2671	(0.0919)	2.8318	(1.1597)	3.4151	(0.2075)	4.3619	(0.8865)	3.7757	(0.2385)	4.9616	(0.5421)
Mean	3.3250	(0.1420)	2.2800	(0.2650)	3.0797	(0.2974)	4.3122	(0.6459)	3.4218	(0.2636)	4.6708	(0.9980)
Overall Mean.	3.3203	(0.1591)	3.0057	(2.0087)	3.3918	(0.3595)	4.9538	(1.5354)	3.9115	(0.4132)	5.4577	(0.9390)
F-test[1]:Env.	NS		NS		*		NS		**		(*)	
Gen.	NS		NS		NS		NS		NS		NS	
GxE.	NS		**		(*)		*		NS		**	

NA : Not applicable;

Least square means within each column within each environment which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;

* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

Table 24. The levels of the three types of α-amylases activities at harvest ripeness and at embryo maturity of six generations of wheat cross Tordo x Karamu (Cross 1) averaged across two environments (in log mEU/g).

Generations	Base α-amylase		Germinative α-amylase		GA3 α-amylase	
	at HR	at embryo maturity	at HR	at embryo maturity	at HR	at embryo maturity
Tordo	3.3397 (0.0650)	NA (-)	3.0321 (0.1467)	NA (-)	3.4127 (0.1687)	NA (-)
Karamu	3.2210 (0.0650)	2.4971 (0.9369)	3.0590 (0.1467)	4.7603 (0.7162)	3.8845 (0.1687)	4.7789 (0.4381)
F_2	3.3554 (0.0650)	3.8044 (0.9369)	3.3937 (0.1467)	5.0472 (0.7162)	3.7642 (0.1687)	6.2483 (0.4381)
F_3	3.4250 (0.0650)	3.0285 (0.8200)	3.8137 (0.1467)	4.7616 (0.6268)	4.1489 (0.1687)	4.9532 (0.3833)
BC_1(Tordo)S_1	3.3532 (0.0650)	4.3762 (0.8200)	3.6254 (0.1467)	5.1934 (0.6268)	3.8855 (0.1687)	5.6364 (0.3833)
BC_1(Karamu)S_1	3.2275 (0.0650)	2.8701 (0.8200)	3.4269 (0.1467)	4.9248 (0.6268)	4.3728 (0.1687)	5.6766 (0.3833)
Mean	3.3203 (0.1591)	5.2798 (2.0087)	3.3918 (0.3595)	5.4532 (1.5354)	3.9114 (0.4132)	5.9551 (0.9390)
Significant generation effect[1] :	NS	NS	NS	NS	NS	NS

NA : Not applicable

1 NS : Non significant.

Values in parentheses are the standard errors of the estimates.

In Table 23 the three α-amylases at embryo maturity of cultivar Tordo are not included in the table because of unusually high extrapolated levels (27.4574,11.5875 and 12.2135, in ln mEU/g, for base α-amylase, germinative α-amylase and GA_3 α-amylase respectively). The apparent high levels of α-amylases at embryo maturity of Tordo were due to the lateness of embryo maturity. The mean values averaged across environments for these three variables for cultivar Tordo are thus also left out from Table 24.

Grain developed in the cool environment had significantly lower germinative α-amylase and GA α-amylase compared to grains developed in the warm environment. There were significant generation x environment interactions for the three α-amylases at embryo maturity and for germinative α-amylase at harvest ripeness. The interactions for the first three variables (three α-amylases at embryo maturity) can not be interpreted directly since, the combined analyses of variance included the abnormally high values of Tordo in the warm environment in the analysis. For germinative α-amylase at harvest ripeness, the F_2, F_3 , BC_1(Tordo)S_1 generations had higher mean values compared to the two parental generations and BC_1(Karamu)S_1 which formed another group with similar means. The differences among generations for this character were manifested in only the warm environment.

Comparisons between α-amylase activities at the harvest ripeness and at embryo maturity were carried out using t-tests. The t-test results are presented in Table 25. Simple correlations between α-amylase activities at the two stages of development were also computed and the correlation coefficients are presented in Table 26. The level of base α-amylase at harvest ripeness is not necessarily lower than at embryo maturity. The paired t-test showed that the base α-amylase levels at the two stages were not significantly different (Table 25).

Table 25. Similarity and dissimilarity of base α-amylase, germinative α-amylase and GA3 α-amylase levels at harvest ripeness and at embryo maturity of cross 1 wheat as a result of paired t-tests.

	Base α-amylase at embryo maturity	Germinative α-amylase at embryo maturity	Germinative α-amylase at harvest ripeness	GA α-amylase at embryo maturity	GA α-amylase at harvest ripeness
Base α-amylase at harvest ripeness	1.21 NS 33	5.34 ** 35	0.75 NS 35	6.64 ** 35	5.00 ** 35
Base α-amylase at embryo maturity		7.94 ** 33	1.03 NS 33	5.91 ** 33	0.42 NS 33
Germinative α-amylase at embryo maturity			5.30 ** 35	0.85 NS 35	4.04 ** 35
Germinative α-amylse at harvest ripeness				6.65 ** 35	4.45 ** 35
GA amylase at embryo maturity					5.18 ** 35

NS : non significant t-values at the 5 % probability level.
** : significant t-values at the 1 % probability level.

Table 26. Correlations between α-amylases at harvest ripeness α-amylase at embryo maturity and germination percentags at harvest ripeness in wheat cross 1.

	Base α-amylase at embryo maturity	Germinative α-amylase at embryo maturity	Germinative α-amylase at harvest ripeness	GA α-amylase at embryo maturity	GA α-amylase at harvest ripeness	Standard germination at harvest ripeness	Potential germination at harvest ripeness
Base α-amylase at harvest ripeness	0.23 NS 34 [a]	0.14 NS 36	0.17 NS 36	0.00 NS 36	0.11 NS 36	0.11 NS 29	-0.23 NS 32
Base α-amylase at embryo maturity		0.86 ** 34	0.22 NS 34	0.63 ** 34	0.23 NS 34	-0.07 NS 27	0.08 NS 30
Germinative α-amylase at embryo maturity			0.24 NS 36	0.75 ** 36	0.18 NS 36	-0.13 NS 29	-0.08 NS 32
Germinative α-amylase at harvest ripeness				0.23 NS 36	0.42 * 36	0.67 ** 29	0.38 * 32
GA α-amylase at embryo maturity					0.16 NS 36	-0.22 NS 29	-0.03 NS 32
GA α-amylase at harvest ripeness						0.35 NS 29	0.74 ** 32
Standard germination at harvest ripeness							0.69 ** 25

NS correlation coefficient was not significant at the 5 % probability level.
* correlation coefficient was significant at the 5 % probability level.
** correlation coefficient was significant at the 1 % probability level.
a number in second row are the sample sizes

IV.2) Cross 2's Results

The changes in base α-amylase, germinative α-amylase and GA_3 α-amylase levels in the six generations of wheat cross 2 (Tordo x Gabo) are presented in Figures A.31, A.33 and A.35 for those ripened in the warm environment and in Figures A.32, A.34 and A.36 for those ripened in the cool environment. The three types of α-amylase at harvest ripeness and at embryo maturity for each of the six generations in each of the two ripening environments are presented in Table 27. The mean values averaged over the two environments are presented in Table 28.

Table 27. The levels of the three types of α-amylases activities at harvest ripeness and at embryo maturity of six generations of wheat in cross Tordo x Gabo (cross 2) grown in the two environments (in log. mEU/g).

Generation	Base α-amylase				Germinative α-amylase				GA3 α-amylase			
	at HR		at embryo maturity		at HR		at embryo maturity		at HR		at embryo maturity	
					WARM ENVIRONMENT							
Tordo	3.1211^{c}	(0.2577)	3.6531	(1.2541)	2.7187^{d}	(0.3415)	4.2066	(1.6568)	2.6788^{e}	(0.3422)	3.4749^{b}	(0.9256)
Gabo	6.3958^{a}	(0.2577)	6.1811	(1.2541)	6.2812^{a}	(0.3415)	5.8565	(1.6568)	6.9812^{a}	(0.3422)	7.4834^{a}	(0.9256)
F_2	4.5594^{b}	(0.2577)	4.6914	(0.9838)	4.0307^{bc}	(0.3415)	5.9309	(1.2997)	5.5439^{c}	(0.3422)	6.6728^{a}	(0.7261)
F_3	4.3310^{b}	(0.2577)	4.5133	(0.9838)	3.3853^{cd}	(0.3415)	5.7320	(1.2997)	6.2736^{abc}	(0.3422)	6.6986^{a}	(0.7261)
BC_1 (Tordo) S_1	3.4562^{c}	(0.2577)	5.1172	(0.9838)	3.5011^{bcd}	(0.3415)	6.3117	(1.2997)	4.5451^{d}	(0.3422)	6.5472^{a}	(0.7261)
BC_1 (Gabo) S_1	4.5050^{b}	(0.2577)	4.3740	(0.9838)	4.2319^{b}	(0.3415)	4.7884	(1.2997)	6.4927^{ab}	(0.3422)	6.8717^{a}	(0.7261)
Mean	4.3947	(0.5404)	4.7550	(1.3613)	4.0248	(0.6020)	5.4710	(1.2785)	5.4192	(0.5528)	6.2914	(0.4881)
					COOL ENVIRONMENT							
Tordo	2.8738^{c}	(0.2577)	1.7678	(1.2444)	3.5231	(0.3415)	4.7484	(1.6440)	3.3876^{b}	(0.3422)	4.3815	(0.9202)
Gabo	3.9307^{a}	(0.2577)	5.8985	(0.9838)	4.2233	(0.3415)	5.1626	(1.2997)	4.6385^{a}	(0.3422)	4.1786	(0.7261)
F_2	3.2714^{bc}	(0.2577)	3.7661	(0.9838)	3.4338	(0.3415)	7.4148	(1.2997)	4.6308^{a}	(0.3422)	7.3889	(0.7261)
F_3	3.6047^{ab}	(0.2577)	4.1179	(0.9838)	3.5713	(0.3415)	8.4197	(1.2997)	4.9836^{a}	(0.3422)	6.2893	(0.7261)
BC_1 (Tordo) S_1	3.0623^{bc}	(0.2577)	4.7440	(0.9838)	2.7779	(0.3415)	5.4677	(1.2997)	3.6334^{b}	(0.3422)	6.7895	(0.9202)
BC_1 (Gabo) S_1	3.3544^{abc}	(0.2577)	2.9864	(0.9838)	3.2987	(0.3415)	3.7150	(1.2997)	4.7600^{a}	(0.3422)	4.3137	(0.7261)
Mean	3.3495	(0.3263)	3.8801	(1.9589)	3.4713	(0.5809)	5.8214	(2.8495)	4.3390	(0.6300)	5.5569	(1.7104)
Over all mean	3.8721	(0.4463)	4.3176	(1.7040)	3.7481	(0.5915)	5.6462	(2.2512)	4.8791	(0.5927)	5.9242	(1.2577)
F-test[1]:Env.	*		*		NS		NS		(*)		NS	
Gen.	(*)		**		NS		NS		(*)		NS	
GxE.	*		NS		**		NS		**		(*)	

Least square means within each column within each environment which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;

* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

Table 27 showed that grains developed in the warm ripening environment had significantly higher base α-amylase at harvest ripeness and at embryo maturity. Also overall GA3 α-amylase levels at harvest ripeness of grains developed in the warm environment was significantly higher ($P < 0.10$) than that of the grains developed in the cool environment.

Table 28. The levels of the three types of α-amylases activities at harvest ripeness and at embryo maturity of six generations of wheat cross Tordo x Gabo (Cross 2) averaged across two environments (in log mEU/g).

Generations	Base α-amylase				Germinative α-amylase				GA3 α-amylase			
	at HR		at embryo maturity		at HR		at embryo maturity		at HR		at embryo maturity	
Tordo	2.9974^{c}	(0.1822)	2.7105^{c}	(0.8834)	3.1209	(0.2415)	4.4775	(1.1670)	3.3033^{a}	(0.2420)	3.9282	(0.6526)
Gabo	5.1633^{a}	(0.1822)	6.0398^{a}	(0.7970)	5.2522	(0.2415)	5.5095	(1.0529)	5.8098^{a}	(0.2420)	5.8310	(0.5882)
F_2	3.9154^{b}	(0.1822)	4.2288^{abc}	(0.6957)	3.7323	(0.2415)	6.6727	(0.9190)	5.0874^{b}	(0.2420)	7.0309	(0.5135)
F_3	3.9678^{b}	(0.1822)	4.3156^{abc}	(0.6957)	3.4783	(0.2415)	7.0759	(0.9190)	5.6286^{ab}	(0.2420)	6.4940	(0.5135)
BC_1(Tordo)S_1	3.2592^{c}	(0.1822)	4.9306^{ab}	(0.6957)	3.1395	(0.2415)	5.8897	(0.9190)	4.0893^{c}	(0.2420)	6.6684	(0.5861)
BC_1(Gabo)S_1	3.9297^{b}	(0.1822)	3.6802^{bc}	(0.6957)	3.7653	(0.2415)	4.2517	(0.9190)	5.6263^{ab}	(0.2420)	5.5927	(0.5135)
Mean	3.8721	(0.4463)	4.3176	(1.7040)	3.7481	(0.5915)	5.6462	(2.2512)	4.8791	(0.5927)	5.9242	(1.2577)
Significant generation effect[1] :	(*)		**		NS		NS		(*)		NS	

Least square means within each column which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;

* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

The overall means of generations were significantly different for base α-amylase at embryo maturity ($P < 0.01$) and for base α-amylase, and GA3 α-amylase at harvest ripeness ($P < 0.10$). Generation x environment interactions were significant for base α-amylase and germinative α-amylase at harvest ripeness and for GA3 α-amylase at both stages. In this cross, except for germinative α-amylase in the cool environment, Tordo had a lower level of all types of α-amylase activity at harvest ripeness compared to Gabo in both environments.

Averaged over the two environments, Gabo also showed higher means for base α-amylase at harvest ripeness and at embryo maturity and GA3 α-amylase at harvest ripeness compared to Tordo.

Table 29 shows the t-values for comparison between α-amylase activities of wheat cross 2 at the two stages of development. Simple correlation coefficients between pairs of α-amylase activities are presented in Table 30. The paired t-test for the difference between base α-amylase at harvest ripeness and at embryo maturity in this cross showed that the base α-amylase levels at the two different times were significantly different (Table 29)

Table 29. Similarity and dissimilarity of base α-amylase, germinative α-amylase and GA3 α-amylase levels at harvest ripeness and at embryo maturity of cross 2 wheat as a result of paired t-tests.

	Base α-amylase at embryo maturity	Germinative α-amylase at embryo maturity	Germinative α-amylase at harvest ripeness	GA α-amylase at embryo maturity	GA α-amylase at harvest ripeness
Base α-amylase at harvest ripeness	2.49 * 35[a]	4.92 ** 35	1.14 NS 35	6.19 ** 33	6.87 ** 35
Base α-amylase at embryo maturity		3.25 ** 35	2.81 ** 35	2.83 ** 33	0.22 NS 35
Germinative α-amylase at embryo maturity			5.18 ** 35	0.43 NS 33	2.42 NS 35
Germinative α-amylase at harvest ripeness				6.07 ** 33	6.89 ** 35
GA α-amylase at embryo maturity					2.98 ** 33

NS : non significant t-values at the 5 % probability level.
* : significant t values at the 5 % probability level.
** : significant t-values at the 1 % probability level.
a : Numbers on the second row of each cell are sample sizes.

Table 30. Correlations between α-amylases at harvest ripeness, α-amylase at embryo maturity and germination percentags at harvest ripeness in wheat cross 2.

	Base α-amylase at embryo maturity	Germinative α-amylase at embryo maturity	Germinative α-amylase at harvest ripeness	GA α-amylase at embryo maturity	GA α-amylase at harvest ripeness	Standard germination at harvest ripeness	Potential germination at harvest ripeness
Base α-amylase at harvest ripeness	0.17 NS 36[a]	0.04 NS 36	0.80 ** 36	0.26 NS 34	0.77 ** 36	0.55 ** 33	0.67 ** 33
Base α-amylase at embryo maturity		0.48 ** 36	0.16 NS 36	-0.07 NS 34	-0.11 NS 36	0.05 NS 33	0.12 NS 33
Germinative α-amylase at embryo maturity			0.03 NS 36	0.13 NS 34	-0.08 NS 36	0.05 NS 33	0.11 NS 33
Germinative α-amylase at harvest ripeness				0.11 NS 34	0.70 ** 36	0.59 ** 33	0.49 ** 33
GA α-amylase at embryo maturity					0.49 ** 34	0.22 NS 31	0.57 ** 31
GA α-amylase at harvest ripeness						0.61 ** 33	0.79 ** 33
Standard germination at harvest ripeness							0.60 ** 31

NS correlation coefficient was not significant at the 5 % probability level.
* correlation coefficient was significant at the 5 % probability level.
** correlation coefficient was significant at the 1 % probability level.
a : Numbers in the second row of each cell are the sample sizes.

Table 30 showed that the base α-amylase level was correlated with both germinative a-amylase and GA α-amylase levels at harvest ripeness. At embryo maturity the base α-amylase level correlated with germinative α-amylase level only. The germinative and GA α-amylase levels at harvest ripeness correlated with both the standard and potential germinations. The two germination percentages were also closely correlated.

IV.3) Cross's 3 Results

The changes in levels of base α-amylase, germinative α-amylase and GA_3 α-amylase of the six generations of wheat cross 3 (Tordo x Sonora 64A) developed in the warm ripening environment are presented in Figures A.37, A.39 and A.41 respectively. Likewise, the levels of these three α-amylases of the six generations ripening in the cool environment are presented in Figures A.38, A.40 and A.42. The mean values of base α-amylase, germinative α-amylase and GA_3 α-amylase at two stages of developments i.e. harvest ripeness and at embryo maturity are presented in Table 31. The mean values of the six variables for each of the six generations averaged over the two environments are presented in Table 32.

Table 31. The levels of the three types of α-amylases at harvest ripeness and at embryo maturity of six generations of wheat in cross Tordo x Sonora 64A (cross 3) grown in the two environments (in log. mEU/g).

Generation	Base α-amylase				Germinative α-amylase				GA3 α-amylase			
	at HR		at T90PG		at HR		at T90PG		at HR		at T90PG	
WARM ENVIRONMENT												
Tordo	3.2416	(0.1416)	7.7144[a]	(0.4539)	3.2760[c]	(0.3404)	1.0823	(1.6640)	3.2671[c]	(0.4061)	6.3709	(1.0525)
Sonora 64A	3.3532	(0.1416)	3.5272[b]	(0.6546)	5.5059[a]	(0.2670)	5.1700	(1.6640)	6.4447[a]	(0.4061)	6.4102	(1.5123)
F_2	3.5723	(0.1416)	3.3072[b]	(0.3516)	4.3788[b]	(0.2670)	4.5596	(0.8842)	5.4400[b]	(0.4061)	5.7809	(0.8109)
F_3	3.5301	(0.1416)	3.4492[b]	(0.3516)	4.4642[b]	(0.2670)	5.6943	(0.8842)	5.7914[ab]	(0.4061)	7.4319	(0.8109)
BC_1(Tordo)S_1	3.5340	(0.1416)	3.2049[b]	(0.3516)	3.4069[c]	(0.3404)	4.1041	(0.8842)	5.1042[b]	(0.5137)	7.0694	(1.0423)
BC_1(Sonora)S_1	3.4029	(0.1416)	3.4250[b]	(0.4539)	4.4074[b]	(0.2670)	5.1371	(1.1415)	5.7995[ab]	(0.4061)	3.3408	(1.0525)
	3.4390	(0.3077)	4.1046	(0.5121)	4.2399	(0.5179)	4.2912	(2.3203)	5.3078	(0.8900)	6.0673	(2.1625)
COOL ENVIRONMENT												
Tordo	3.3524	(0.1416)	2.6441	(0.3516)	2.9189	(0.2670)	5.4690	(0.8842)	3.0715[b]	(0.4061)	6.0245	(0.8109)
Sonora 64A	3.0500	(0.1416)	3.9494	(0.3516)	3.1824	(0.2670)	3.9603	(0.8842)	4.0126[ab]	(0.4061)	5.9104	(0.8109)
F_2	3.2941	(0.1416)	3.0086	(0.3516)	3.3303	(0.2670)	4.9601	(0.8842)	4.3607[a]	(0.4061)	6.7138	(0.8109)
F_3	3.3251	(0.1416)	3.1689	(0.3516)	3.4152	(0.2670)	4.5644	(0.8842)	4.4880[a]	(0.4061)	6.5880	(0.8109)
BC_1(Tordo)S_1	3.2938	(0.1416)	3.4533	(0.3516)	2.9850	(0.2670)	4.7414	(1.1184)	4.4960[a]	(0.4061)	7.2480	(0.8109)
BC_1(Sonora)S_1	3.1973	(0.1416)	2.7372	(0.3516)	3.2456	(0.2670)	5.4987	(0.8842)	4.4541[a]	(0.4061)	7.6547	(0.8109)
Mean	3.2521	(0.1600)	3.1602	(0.6602)	3.1796	(0.4129)	4.8656	(0.8108)	4.1471	(0.4766)	6.6899	(0.7878)
Overall mean.	3.3456	(0.2453)	3.6324	(0.6089)	3.7097	(0.4625)	4.5784	(1.5315)	4.7275	(0.7034)	6.3786	(1.4045)
F-test[1] :Env.	*		NS		*		NS		*		NS	
Gen.	NS		NS		NS		NS		(*)		NS	
GxE.	NS		**		*		NS		NS		NS	

Least square means within each column within each environment which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level;

* : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the estimates.

Table 31 shows that grains developed in the warm ripening environment had higher levels of base α-amylase, germinative α-amylase and GA_3 α-amylase at harvest ripeness than the same types of α-amylases of grains developed in the cool ripening environment. Generation means averaged over the two environments were significantly different only for GA_3 α-amylase at harvest ripeness ($P < 0.10$). GA_3 α-amylase of Tordo was significantly lower than those of other generations. Generation x environment interaction were significant for base α-amylase at embryo maturity and germinative α-amylase at harvest ripeness. Both characters showed significant differences among generations only in the warm ripening environment.

Table 32. The levels of the three types of α-amylases at harvest ripeness and at embryo maturity of six generations of wheat cross Tordo x Sonora 64A (Cross 3) averaged across two environments (in log mEU/g).

Generations	Base α-amylase		Germinative α-amylase		GA3 α-amylase	
	at HR	at T90PG	at HR	at T90PG	at HR	at T90PG
Tordo	3.2970 (0.1001)	5.1793 (0.2871)	3.0975 (0.2163)	3.2757 (0.9422)	3.1693[b] (0.2872)	6.1977 (0.6643)
Sonora 64A	3.2016 (0.1001)	3.7383 (0.3715)	4.3441 (0.1888)	4.5652 (0.9422)	5.2287[a] (0.2872)	6.1603 (0.8580)
F_2	3.4332 (0.1001)	3.1579 (0.2486)	3.8546 (0.1888)	4.7599 (0.6252)	4.9004[a] (0.2872)	6.2473 (0.5734)
F_3	3.4276 (0.1001)	3.3091 (0.2486)	3.9397 (0.1888)	5.1294 (0.6252)	5.1397[a] (0.2872)	7.0063 (0.5734)
BC_1(Tordo)S_1	3.4139 (0.1001)	3.3291 (0.2486)	3.1959 (0.2163)	4.4228 (0.7129)	4.8001[a] (0.2872)	7.1587 (0.6603)
BC_1(Sonora)S_1	3.3000 (0.1001)	3.0811 (0.2871)	3.8265 (0.1888)	5.3179 (0.7129)	5.1269[a] (0.3274)	5.4977 (0.6643)
Mean	3.3456 (0.2453)	3.3625 (0.6089)	3.7097 (0.4625)	4.5784 (1.5315)	4.7275 (0.7034)	6.3780 (1.4045)
Significant generation effect[1] :	NS	NS	NS	NS	(*)	NS

Least square means within each column which have a common letter are not significantly different by t-test at the 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level.

Values in parentheses are the standard errors of the estimates.

Comparisons between pairs of α-amylase activities by t-tests were carried out, and the results are presented in Table 33. Table 33 showed that base α-amylase levels at harvest ripeness and at embryo maturity were not significantly different. While germinative α-amylase levels as well as GA_3 amylase levels at the two stages of development were significantly different.

Table 33. Similarity and dissimilarity of base α-amylase, germinative α-amylase and GA3 α-amylase levels at harvest ripeness and at embryo maturity of cross 3 wheat as a result of paired t-tests.

	Base α-amylase at embryo maturity	Germinative α-amylase at embryo maturity	Germinative α-amylase at harvest ripeness	GA α-amylase at embryo maturity	GA α-amylase at harvest ripeness
Base α-amylase at harvest ripeness	2.21 NS 35	6.79 ** 31	2.39 * 33	21.04 ** 32	7.09 ** 34
Base α-amylase at embryo maturity		6.84 ** 31	1.12 NS 33	6.19 ** 32	1.12 NS 34
Germinative α-amylase at embryo maturity			5.76 ** 31	3.24 ** 29	2.35 * 31
Germinative α-amylase at harvest ripeness				12.75 ** 31	8.75 ** 33
GA α-amylase at embryo maturity					8.28 ** 32

NS : non significant t-values at the 5 % probability level.
* : significant t values at the 5 % probability level.
** : significant t-values at the 1 % probability level.

The correlations between α-amylase activities and the two germinations at harvest ripeness were also computed. The simple correlation coefficients among these variables are presented in Table 34. Table 34 shows that among α-amylase activities estimated, base α-amylase and germinative α-amylase at embryo maturity were highly correlated. Also germinative α-amylase and GA α-amylase at harvest ripeness were highly correlated. The germinative α-amylase and GA α-amylase at harvest ripeness are both highly correlated with the two germination percentages.

Table 34. Correlations between α-amylases at harvest ripeness, α-amylase at embryo maturity and germination percentags at harvest ripeness in wheat cross 3.

	Base α-amylase at embryo maturity	Germinative α-amylase at embryo maturity	Germinative α-amylase at harvest ripeness	GA α-amylase at embryo maturity	GA α-amylase at harvest ripeness	Standard germination at harvest ripeness	Potential germination at harvest ripeness
Base α-amylase at harvest ripeness	-0.13 NS 36	0.01 NS 32	0.06 NS 34	-0.09 NS 33	0.17 NS 35	-0.13 NS 35	0.17 NS 32
Base α-amylase at embryo maturity		0.80 ** 32	0.26 NS 34	-0.08 NS 33	0.05 NS 35	0.28 NS 35	-0.05 NS 32
Germinative α-amylase at embryo maturity			0.28 NS 32	0.23 NS 30	0.18 NS 32	0.34 NS 31	-0.11 NS 28
Germinative α-amylase at harvest ripeness				-0.12 NS 32	0.79 ** 34	0.52 ** 33	0.77 ** 30
GA α-amylase at embryo maturity					0.13 NS 33	-0.03 NS 32	0.07 NS 30
GA α-amylase at harvest ripeness						0.53 ** 34	0.84 ** 31
Standard germination at harvest ripeness							0.45 * 31

NS correlation coefficient was not significant at the 5 % probability level..
* correlation coefficient was significant at the 5 % probability level.
** correlation coefficient was significant at the 1 % probability level.
a : Numbers in the second row of each cell are the sample sizes

V) MAXIMUM COLOUR SCORE

Changes in colour scores during grain development of the six generations in each of the three wheat crosses ripened in the warm and in the cool environments are presented in Figures A.43 and A.44 respectively, those for cross 2 in Figures A.45 and A.46, and for cross 3 in Figures A.47 and A.48.

The maximum colour scores of each of the six generations of each of the three crosses developed in the two ripening environments are presented in Table 35. Data for this variable averaged over the two environments for all the three crosses are presented in Table 36. In both Table 35 and Table 36, generation label P_1 means Tordo and $BC_1(P_1)S_1$ means BC_1(Tordo)S_1. Thus P_2 means Karamu, Gabo, and Sonora 64A in crosses 1, 2 and 3 respectively and the generation $BC_1(P_2)S_1$ are the selfed backcrosses to coresponding P_2. Note that this labelling is independent to the allocation of two parents as P_1 and P_2 in generation mean analysis in the following chapter.

Table 35. Maximum colour scores of each of the six generations in the three wheat crosses grown in the two environments.

Env.	Gen.	Cross 1		Cross 2		Cross 3	
Warm	P_1	2.67^{c}	(0.09)	2.60^{b}	(0.04)	2.50^{e}	(0.04)
	P_2	3.58^{a}	(0.09)	2.74^{a}	(0.04)	3.22^{a}	(0.04)
	F_2	3.06^{b}	(0.09)	2.75^{a}	(0.04)	2.90^{c}	(0.05)
	F_3	3.15^{b}	(0.09)	2.76^{a}	(0.04)	2.76^{d}	(0.04)
	$BC_1(P_1)S_1$	3.14^{b}	(0.09)	2.59^{b}	(0.04)	2.86^{c}	(0.04)
	$BC_1(P_2)S_1$	3.43^{a}	(0.09)	2.64^{b}	(0.04)	3.11^{b}	(0.04)
Warm env. mean		3.17	(0.11)	2.68	(0.06)	2.89	(0.06)
Cool	P_1	2.77^{d}	(0.09)	2.58^{b}	(0.04)	2.60^{d}	(0.04)
	P_2	3.48^{a}	(0.09)	2.77^{a}	(0.04)	3.19^{a}	(0.04)
	F_2	3.10^{bc}	(0.09)	2.76^{a}	(0.04)	3.04^{b}	(0.04)
	F_3	3.14^{bc}	(0.09)	2.77^{a}	(0.04)	2.97^{b}	(0.04)
	$BC_1(P_1)S_1$	3.01^{c}	(0.09)	2.63^{b}	(0.04)	2.83^{c}	(0.04)
	$BC_1(P_2)S_1$	3.29^{ab}	(0.09)	2.77^{a}	(0.04)	3.00^{b}	(0.04)
Cool env. mean		3.13	(0.20)	2.71	(0.08)	2.94	(0.06)
Overall mean		3.15	(0.16)	2.70	(0.07)	2.92	(0.06)
F-test results[1]	:Env.	NS		NS		NS	
	Gen.	**		*		**	
	G x E.	NS		NS		**	

Least square means within each column within each environment which have a common letter are not significant different by t-test at the 10 % probability level.
1 NS : Non significant; * : significant at the 5 % probability level; ** : significant at the 1 % probability level.
Values in parentheses are the standard errors of the least square means.

Table 35 showed that ripening environment had no effect on the expression of colour scores. The generation effects were significant in all crosses. Averaged over the two environments, Tordo had a significantly lower maximum colour score than the other parents (Karamu, Gabo and Sonora 64A) in all the three crosses. It is noteworthy that cross 2, involving only white wheats, still showed a significant generation difference for colour, but all values were within the "white" range. The other two crosses each involved apparent one gene differences in the classical "red" genes (see Materials and Methods). For these two crosses, notice particularly that the means for F_2 are not at the level of $(3(P_1) + 1(P_2))/4$ as would be expected if only the one classical gene for redness was operating. This will be discussed further later.

Table 36. Maximum colour scores of each of the six generations in the three wheat crosses, averaged across two environments.

Generations	Cross 1		Cross 2		Cross 3	
P_1	2.72	(0.06)	2.59	(0.03)	2.55	(0.03)
P_2	3.53	(0.06)	2.76	(0.03)	3.21	(0.03)
F_2	3.08	(0.06)	2.76	(0.03)	2.97	(0.03)
F_3	3.15	(0.06)	2.77	(0.03)	2.87	(0.03)
$BC_1(P_1)S_1$	3.08	(0.06)	2.61	(0.03)	2.84	(0.03)
$BC_1(P_2)S_1$	3.36	(0.06)	2.70	(0.03)	3.05	(0.03)
Mean	3.15	(0.16)	2.70	(0.07)	2.92	(0.06)
Significance of generation effect[1] :	**		*		**	

1 * : significant at the 5 % probability level; ** : significant at the 1 % probability level.
Values in parentheses are the standard errors of the least square means.

VI) STERILITY PERCENTAGE

The sterility percentages, i.e. percentage of undeveloped grains in the sampled portions of the ear, of each of the six generations in the three crosses grown in the two environments are presented in Table 37. The mean values averaged over the two environments are presented in Table 38. The rule for labeling the P_1 and P_2 used for maximum colour score also applied to this character (i.e.- P_1 is Tordo throughout).

Table 37. Sterility percentages of each of the six generations in the three wheat crosses grown in two environments.

Env.	Gen.	Cross1		Cross2		Cross3	
Warm	P_1	15.41^{a}	(1.59)	10.43^{b}	(2.70)	13.90^{a}	(2.44)
	P_2	7.60^{bc}	(1.59)	21.50^{a}	(2.70)	3.57^{c}	(2.44)
	F_2	5.80^{c}	(1.59)	20.90^{a}	(2.70)	6.22^{c}	(2.44)
	F_3	10.03^{b}	(1.59)	13.74^{b}	(2.70)	12.45^{ab}	(2.44)
	$BC_1(P_1)S_1$	16.89^{a}	(1.59)	23.28^{a}	(2.70)	15.29^{a}	(2.44)
	$BC_1(P_2)S_1$	5.80^{c}	(1.59)	12.11^{b}	(2.70)	7.23^{bc}	(2.44)
Warm env. mean		10.26	(2.87)	16.99	(5.91)	9.77	(4.93)
Cool	P_1	4.99^{bc}	(1.59)	5.18^{a}	(2.70)	7.17	(2.44)
	P_2	2.61^{c}	(1.59)	6.63^{ab}	(2.70)	1.11	(2.44)
	F_2	3.68^{c}	(1.59)	3.48^{b}	(2.70)	6.27	(2.44)
	F_3	8.68^{ab}	(1.59)	4.39^{b}	(2.70)	7.20	(2.44)
	$BC_1(P_1)S_1$	11.37^{a}	(1.59)	11.12^{a}	(2.70)	9.35	(2.44)
	$BC_1(P_2)S_1$	3.38^{c}	(1.59)	5.52^{ab}	(2.70)	5.27	(2.44)
Cool env. mean		5.79	(2.63)	6.05	(2.94)	6.15	(3.38)
Overall mean		8.02	(2.75)	11.52	(4.67)	7.96	(4.22)
F-test results[1]:	Env.	*		**		*	
	Gen.	*		NS		*	
	G x E.	(*)		NS		NS	

Least square means within each column within each environment which have a common letter are not significant different by t-test at 10 % probability level.

1 NS : Non significant; (*) : significant at the 10 % probability level; * : significant at the 5 % probability level; ** : significant at the 1 % probability level.

Values in parentheses are the standard errors of the least square means.

Table 37 shows that in all crosses, the warm environment during the grain development period caused significantly higher sterility than the cool ripening environment. Generation effects were significant in two out of the three crosses. In these two crosses (1 and 3), Tordo had a higher percent sterility than the other parents.

Table 38. Sterility percentages of each of the six generations in the three wheat crosses, averaged across two environments.

Generations	Cross 1		Cross 2		Cross 3	
P_1	10.20	(1.12)	7.81	(1.91)	10.54	(1.72)
P_2	5.11	(1.12)	14.06	(1.91)	2.34	(1.72)
F_2	4.75	(1.12)	12.19	(1.91)	6.25	(1.72)
F_3	9.36	(1.12)	9.07	(1.91)	9.83	(1.72)
$BC_1(P_1)S_1$	14.13	(1.12)	17.20	(1.91)	12.32	(1.72)
$BC_1(P_2)S_1$	4.59	(1.12)	8.82	(1.91)	6.50	(1.72)
Mean	8.02	(2.75)	11.52	(4.67)	7.96	(4.22)
Significance of generation effects[1] :	*		NS		*	

1 NS : Non significant; * : significant at the 5 % probability level. Values in parentheses are the standard errors of the least square means.

VII) GENERATION MEAN ANALYSIS

Gene effects controlling characters related to maturity and characters with some relevance to sprouting damage will be discussed in this section. The parameter estimates from the twelve parameter model are presented for all characters, except base α-amylase, germinative α-amylase and GA α-amylase at embryo maturity in cross 1 (because the estimated mean values for these characters of Tordo was abnormally high).

The analysis of gene effects using a six parameter model for the generation means averaged from the two environments was also carried out. This analysis which included the six parameters into the model (*m, a, d, aa, ad* and *dd*) does not take the environmental effect and its interactions into account, and estimates without bias the mean genetic effects. These results are presented along with the full twelve parameter model for two characters (maximum colour score and germinative α-amylase at HR), in order to check that the twelve parameter model provides unbiased estimates of the mean genetic effects. The maximum colour score was chosen for this presentation because it represented a character which showed significant generation effects in the analysis of variance and was one for which there is considerable knowledge about its classical inheritance. The α-amylase level at harvest ripeness was chosen to represent a character with significant generation x environment interaction. Estimates of gene effects from the six parameter and twelve parameter models are presented in Table 39 (for maximum colour score) and Table 40 for germinative α-amylase at harvest ripeness. Both, Table 39 and Table 40 showed that the estimates of the six genetic parameters (*m, a, d, aa, ad* and *dd*) obtained from the six and twelve parameter models were the same except for small rounding errors. Consequently only the results from the twelve parameter model are presented for the rest of the study because they contain more information.

The discussion will emphasize only the characters which showed significant generation effects or significant generation x environment interaction. The term 'equivocal' will be used in the context that the gene effect was significant when the generation effect or generation x environment interaction was not significant in the analysis of variance. When a significant gene effect was observed in a character that showed significant generation effect or generation x environment interaction, the term 'unequivocal' will be used for this circumstance. In testing the effects, a t-test was employed using standard error estimates and a degree of freedom equal to the error degree of freedom in the analysis of variance (df = 20). The significant levels were selected at 10, 5 and 1 %. The symbols for each significant level are presented at the bottom of each table. The estimates which were not significant by t-test but had values greater than their standard errors were marked with a plus sign (+).

The allocations of the parents as P_1 or P_2 were based on the comparative values of the parental genotypes. The parent with the greater phenotypic value was set as P_1, in accordance with the usual practice with these gene models. Also generation means in the environment with higher environmental mean would have +e (i.e. the e parameter has a coefficient of +1) in their expectations while the generation means in the environment with lower environmental mean will have -e (i.e. the e parameter has a coefficient of -e) in their expectation. The mean expectation of any generation in any environment may be expressed as a linear function of these parameter estimates.

VII.1) Generation Mean Analysis of Maximum Colour Score

The estimation of the components of generation means based on the six and twelve parameter models for maximum colour score are presented in Table 39. The corresponding generation means are presented in Table 36, for six parameter model; and in Table 35, for the twelve parameter model.

Table 39. Estimation of the components of generation means on a six parameter model and twelve parameter model for maximum colour score in the three wheat crosses.

Gene effects	Cross 1 Estimates	s.e.	Cross 2 Estimates	s.e.	Cross 3 Estimates	s.e.
			Maximum Colour Score			
			Six Parameter Model			
m	3.08 **	(0.09)	2.76 **	(0.04)	2.97 **	(0.03)
a	0.16	(0.22)	0.10 +	(0.09)	0.09 --	(0.08)
d	-1.03	(0.67)	0.67 *	(0.30)	0.02	(0.25)
aa	0.28	(0.37)	-0.46 *	(0.17)	0.30	(0.17)
ad	-0.25	(0.22)	0.01	(0.09)	-0.24 *	(0.08)
dd	-3.00 +	(2.22)	2.84 *	(0.99)	-1.52 +	(0.91)
			Twelve Parameter Model			
m	3.08 **	(0.07)	2.76 **	(0.03)	2. / **	(0.04)
a	0.17	(0.23)	0.11 +	(0.10)	0 9 +	(0.08)
d	-1.01 +	(0.61)	0.62 *	(0.28)	-0 3	(0.30)
aa	0.29	(0.40)	-0.43 *	(0.17)	.34 *	(0.16)
ad	-0.24 +	(0.23)	0.03	(0.10)	- .24 **	(0.08)
dd	-3.00 +	(2.34)	2.62 *	(1.00)	- .78 (*)	(0.92)
e	-0.02	(0.07)	0.01	(0.03)	.07 (*)	(0.04)
ae	-0.04	(0.23)	0.08	(0.10)	.05	(0.08)
de	-0.66 +	(0.61)	-0.31 +	(0.28)	.74 *	(0.30)
aae	0.25	(0.40)	0.15	(0.17)	0.56 **	(0.16)
ade	-0.09	(0.23)	0.07	(0.10)	-0.02	(0.08)
dde	-2.24	(2.34)	-1.22 +	(1.00)	3.50 **	(0.92)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

The genetic estimates derived from the six parameter model and twelve parameter model are the same except for small rounding errors. The twelve parameter model also contains the information about the environment and the genetic x environment interaction effects. So this model is preferable.

There were significant generation effects in all three crosses, and a significant generation x environment interaction was detected in cross 3. Cross 1 (Tordo x Karamu) had the mean effect as a sole

significant effect for maximum colour score, but other effects were larger than their standard errors (dominance, additive x dominance dominance x dominance and dominance x environment interaction).

Cross 2 (Tordo x Gabo) in which both parents were white grained wheats, showed a significant mean effect and significant dominance, additive x additive and dominance x dominance effects. Gene effects in this cross clearly were not the classical red genes, but must indicate other genes which are related to the reaction of grain coat to NaOH solution. It appeared that the positive enhancing mean effect of *dd* was balanced out by the negative *aa* effect and by dominance effect since the coefficients for the dominance effect in the expectation of the means were all negative.

The parameters estimated in cross 3 were more complicated than expected. The mean effect together with the additive x dominance effect, *aae* effect and *dde* effect were highly significant, while *aa*, *dd*, and *de* effects were significant at the ~~the~~ 5 % probability level. The environmental effect was also significant at a 10 % probability level. One parent of this cross, Sonora 64A, has only one gene for grain redness (Jan and Qualset, 1976). Because Tordo has none of the classical genes for grain redness the epistasis effects found in this cross must be due to hitherto unreported modifiers. There were similarities in the directions of many epistasis effects between cross 1 and cross 3 (e.g. both had the negative effects of *d*, *ad*, *e*, *de*, and *dde*). The negative effects of dominance indicate that white grain coat is dominant or partially dominant to the red grain coat character. All these contradicting results from the earlier reports will be considered further in the Discussion. But briefly, it should be remembered that: (i) this analysis analyses population mean effects, not segregating individual counts; (ii) other genes besides the three "classical" may well be operating; and (iii) this is a quantitative measure of redness not a qualitative one as reported in earlier work.

VII.2) Germinative α-Amylase at Harvest ripeness

The genetic effect, environmental effect and genetic x environment interaction estimated from the six parameter model and the twelve parameter model are presented in Table 40. The mean values corresponding to the six parameter model analyses are presented in Tables 24, 28 and 32 respectively, and the mean values corresponding to the twelve parameter model analyses are presented in Tables 23, 27 and 31.

Table 40. Estimation of the components of generation means on a six-parameter model and twelve parameter model for germinative α-amylase at harvest ripeness in the three wheat crosses.

Gene effects	Cross 1 Estimates		s.e.	Cross 2 Estimates		s.e.	Cross 3 Estimates		s.e.
				Germinative α-Amylase at Harvest Ripeness					
				Six Parameter Model					
m	3.3937	**	(0.1968)	3.7323	**	(0.3260)	3.8546	**	(0.2655)
a	-0.4105		(0.4756)	0.1859		(0.7956)	0.6379		(0.6428)
d	-1.7559	+	(1.5162)	3.1477	+	(2.5215)	2.4796	+	(2.0471)
aa	-1.1502	+	(0.8596)	-0.1036		(1.3876)	-1.7140	+	(1.1666)
ad	-0.4239		(0.4771)	-0.8797	+	(0.7979)	0.0146		(0.6447)
dd	-0.3036		(5.0165)	8.5268	+	(8.2469)	11.2800	+	(6.7922)
				Twelve Parameter Model					
m	3.3937	**	(0.1842)	3.7322	**	(0.2946)	3.8545	**	(0.2438)
a	-0.4106		(0.4842)	0.1859		(0.8199)	0.6377		(0.6592)
d	-1.7560	+	(1.4695)	3.1475	+	(2.4111)	2.4791	+	(1.9694)
aa	-1.1499	+	(0.8731)	-0.1036		(1.4283)	-1.7139	+	(1.1913)
ad	-0.4240		(0.4872)	-0.8798	+	(0.8244)	0.0144		(0.6631)
dd	-0.3050		(5.0635)	8.5266	+	(8.3967)	11.2788	+	(6.8846)
e	0.5726	**	(0.1842)	0.2984	+	(0.2946)	0.5242	*	(0.2438)
ae	-0.8958	(*)	(0.4842)	-0.5056		(0.8199)	0.2483		(0.6592)
de	1.7549	+	(1.4695)	-0.8954		(2.4111)	1.3184		(1.9694)
aae	-0.5803		(0.8731)	2.0284	+	(1.4283)	-0.5143		(1.1913)
ade	-0.8077	+	(0.4872)	-1.2212	+	(0.8244)	-0.2433		(0.6631)
dde	4.3038		(5.0635)	-9.8446	+	(8.3967)	5.2776		(6.8846)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

The genetic estimates from the two models are the same except for very small differences due to rounding error. While the effects estimated from the six parameter model showed no significant gene effects apart from the mean effects in all the three crosses, the estimates from the twelve parameter model showed significant environmental effects in two crosses (cross 1 and cross 3) and an *ae* interaction effect in one cross (cross 1). The dominance effect decreased germinative α-amylase in cross 1 and increased germinative α-amylase in crosses 2 and 3, the effects were not significant, but larger than the standard errors. Additive x additive epistasis decreased germinative α-amylase in cross 1 and 3. Dominance x dominance reinforced the effect of dominance in increasing the value of germinative α-amylase in crosses 2 and 3. Additive x dominance epistasis decreased germinative α-amylase in cross 2.

VII.3) Harvest Ripeness and α-Amylase Maturities

The generation mean analysis results of times to harvest ripeness, α-amylase maturity (PI1) and GA α-amylase maturity (PI2) of the three wheat crosses are presented in Table 41. The corresponding generation means are presented in Tables 1, 4 and 7.

Table 41. Estimation of the components of generation means on a twelve-parameter model for times to harvest ripeness, amylase maturity and GA amylase maturity in the three wheat crosses.

Gene effects	Cross 1 Estimates		s.e.	Cross 2 Estimates		s.e.	Cross 3 Estimates		s.e.
				Harvest Ripeness (HR)					
m	59.09	**	(1.32)	63.54	**	(3.87)	58.41	**	(2.17)
a	-2.29		(3.25)	-4.05		(9.64)	-0.96		(3.62)
d	-9.62		(10.27)	24.78		(30.17)	-4.62		(14.88)
aa	10.02	+	(5.85)	-3.01		(16.56)	1.16		(6.31)
ad	-2.96		(3.28)	-5.39		(9.75)	-1.40		(3.77)
dd	-58.00	+	(34.17)	63.68		(99.09)	-4.80		(39.64)
e	17.05	**	(1.32)	23.89	**	(3.87)	19.94	**	(2.17)
ae	0.63		(3.25)	3.05		(9.64)	3.49		(3.62)
de	-6.54		(10.27)	20.36		(30.17)	-2.42		(14.88)
aae	6.22	+	(5.85)	-8.67		(16.56)	-1.68		(6.31)
ade	0.32		(3.28)	6.19		(9.75)	2.98		(3.77)
dde	-35.12	+	(34.17)	52.40		(99.09)	-4.32		(39.64)
				Amylase Maturity (PI1)					
m	53.71	**	(3.35)	67.81	**	(4.99)	49.43	**	(3.88)
a	8.11		(8.29)	2.50		(12.65)	-3.83		(12.04)
d	2.47		(26.07)	40.93	+	(39.22)	-55.70	+	(33.49)
aa	29.10	(*)	(15.89)	-21.07		(22.09)	36.46	(*)	(20.97)
ad	5.87		(8.53)	0.76		(12.75)	-8.12		(12.08)
dd	-87.40		(89.89)	115.80		(130.77)	-231.94	(*)	(122.29)
e	19.80	**	(3.35)	11.71	*	(4.99)	14.24	**	(3.88)
ae	-2.38		(8.29)	9.93		(12.65)	13.52	+	(12.04)
de	3.47		(26.07)	-38.23		(39.22)	-31.57		(33.49)
aae	16.00	+	(15.89)	-3.47		(22.09)	0.68		(20.97)
ade	-2.31		(8.53)	10.42		(12.75)	13.97	+	(12.08)
dde	-62.60		(89.89)	-80.04		(130.77)	-72.66		(122.29)

Table 41. (continue)

Gene effects	Cross 1 Estimates		s.e.	Cross 2 Estimates		s.e.	Cross 3 Estimates		s.e.
				GA Amylase Maturity (PI2)					
m	51.82	**	(2.04)	50.99	**	(6.20)	41.70	**	(5.78)
a	0.57		(6.22)	-26.12	+	(16.77)	-11.48		(15.43)
d	28.45	+	(17.44)	7.80		(50.09)	-77.62	+	(46.43)
aa	14.79	+	(10.79)	2.61		(32.28)	14.17		(27.34)
ad	-1.27		(6.24)	-32.21	(*)	(16.96)	-15.61	+	(15.49)
dd	1.22		(63.14)	32.40		(180.73)	-133.68		(159.80)
e	15.43	**	(2.04)	14.04	*	(6.20)	17.00	**	(5.78)
ae	-7.10	+	(6.22)	-11.44		(16.77)	-10.11		(15.43)
de	-22.81	+	(17.44)	97.61	(*)	(50.09)	47.82	+	(46.43)
aae	22.19	(*)	(10.79)	-26.97		(32.28)	-15.79		(27.34)
ade	-8.02	+	(6.24)	-15.82		(16.96)	-7.43		(15.49)
dde	-132.42	*	(63.14)	294.20	+	(180.73)	146.96		(159.80)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

The time to harvest ripeness in all the three crosses did not show significant genetic effects. This is probably due to the similarity between the two parents of each cross rather than the lack of any genetic control for this character. The generation mean analyses only showed significant effects of the means (F_2 means) and the environmental effects. In all the three crosses cool environment added 17-24 days to the background means for harvest ripeness (and thus the warm environment subtracted 17-24 days from the background means). This is in concordance with results in Tables 1, 4 and 7 which showed that the differences between environmental means for harvest ripeness were 35, 41 and 39 days for cross 1, cross 2 and cross 3 respectively. According to the model, the difference between the two environmental means in a cross equals twice the environmental effect (*e*).

For amylase maturity, additive x additive epistasis effect increased the means in crosses 1 and 3, while dominance x dominance epistasis decreased the mean only in cross 3. Dominance effect

although not significant, have the increasing effect in cross 2 but have the decreasing effect in cross 3. For this character the gene effects which can be interpreted with certainty were those of cross 1.

GA amylase maturity showed large magnitude of dominance effects in crosses 1 and 3 although the effects were not significant. This gene effect increased the mean in cross 1 and decreased the mean in cross 3. The dominance and *de* effects had opposite signs in crosses 1 and 3, indicated that the dominance effect decreased as the means increased from warm to cool ripening environments.

VII.4) Median Embryo Maturity and Embryo Maturity

The parameters estimated for times to median embryo maturity (T50PG) and embryo maturity (T90PG), of all the three crosses are presented in Table 42. The corresponding generation means are presented in Tables 1, 4 and 7.

Table 42. Estimation of the components of generation means on a twelve-parameter model for times to median embryo maturity (T50PG) and embryo maturity (T90PG) in the three wheat crosses.

Gene effects	Cross 1 Estimates		s.e.	Cross 2 Estimates		s.e.	Cross 3 Estimates		s.e.
				Median Embryo Maturity					
m	73.02	**	(2.54)	80.60	**	(10.28)	74.26	**	(2.40)
a	10.71	+	(7.62)	-37.11	+	(27.54)	15.14	+	(9.07)
d	36.78	+	(21.54)	-14.33		(82.67)	46.54	(*)	(23.15)
aa	19.88	+	(13.95)	40.81		(54.19)	12.22		(16.71)
ad	-5.50		(7.65)	-38.61	+	(28.05)	5.08		(9.11)
dd	22.88		(79.47)	-186.44		(300.48)	66.06		(93.74)
e	24.68	**	(2.54)	28.54	*	(10.28)	28.05	**	(2.40)
ae	6.95		(7.62)	-14.09		(27.54)	1.54		(9.07)
de	14.27		(21.54)	-75.03		(82.67)	16.12		(23.15)
aae	-21.10	+	(13.95)	38.51		(54.19)	-18.70	+	(16.71)
ade	18.83	*	(7.65)	-25.51		(28.05)	10.17	+	(9.11)
dde	55.56		(79.47)	-301.08	+	(300.48)	86.50		(93.74)
				Embryo Maturity					
m	94.67	**	(7.14)	112.55	**	(14.76)	86.49	**	(3.37)
a	15.22		(19.16)	-67.80	+	(40.23)	32.64	*	(12.35)
d	63.69	+	(57.47)	-5.90		(119.66)	-17.22		(31.90)
aa	36.24	+	(34.55)	23.64		(79.26)	21.97		(23.70)
ad	-8.65		(19.31)	-80.04	(*)	(40.78)	23.79	(*)	(12.42)
dd	-17.24		(200.03)	-161.20		(438.60)	-91.12		(130.52)
e	23.38	**	(7.14)	35.86	*	(14.76)	43.24	**	(3.37)
ae	1.43		(19.16)	-14.37		(40.23)	11.13		(12.35)
de	37.07		(57.47)	-90.80		(119.66)	28.11		(31.90)
aae	-65.24	(*)	(34.55)	60.18		(79.26)	12.13		(23.70)
ade	19.25		(19.31)	-21.60		(40.78)	29.36	*	(12.42)
dde	253.08	+	(200.03)	-450.40	+	(438.60)	-38.44		(130.52)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

Median embryo maturity showed significant generation x environment interaction effects in cross 1 and cross 3. In cross 1, the mean and the environmental effects which were highly significant, while the additive x dominance x environment interaction was also significant. This effect decreased the mean of the value of the higher parent and the backcross selfed of this parent in a better environment, it also increased the value of the lower parent and the backcross selfed to this parent in an environment with increasing value. In the environment with decreasing value, the action of *ade* effect is reversed. In cross 1, the genetic effects which were greater than their standard error are additive, dominance, additive x additive (all positive) and additive x additive x environment, which was negative. In cross 3, other than the mean and the environmental effect which were significant, the genetic effect which was important was the dominance effect which was significant at the 10 % probability level. The estimated genetic effects which were not significant but larger than their standard errors were additive, additive x additive x environment and additive x dominance x environment interaction.

Embryo maturity of all the three crosses are significant functions of the means and the environmental effects. Only cross 1 and cross 3 showed significant generation x environment interaction effects. In cross 1 the significant genetic effect was additive x additive x environment. This effect was negative, so its effect was to increase the means of the parental generations and the backcross selfed generations in the environment with a lower mean. The third cross (Tordo x Sonora 64 A) showed significant additive, additive x dominance and additive x dominance x environment effects. All these genetic effects and the genic x environment interaction effect are positive. The two effects *ad* and *ade* will reinforce each other in the environment with higher mean (for this character - cool environment); but they will obliterate each other in the environment with lower mean. In the second cross (Tordo x Gabo) the additive x dominance effect is equivocally significant, despite the non significant generation effects in the analysis of variance.

The parameters estimated for median germination and germination maturity of cross 3 are presented in Table 43. The generation means corresponding to this analysis are presented in Table 7. The estimates for these two characters in cross 1 and cross 2 are not available because means of one generation (Tordo) were undetermined.

Table 43. Estimation of the components of generation means on a twelve-parameter model for times to median germination and germination maturity in cross 3 wheat (Tordo x Sonora 64A).

Gene effects	Cross 3 Estimates		s.e.
	Median Germination		
m	77.92	**	(2.57)
a	14.70	(*)	(7.99)
d	-31.71	+	(22.21)
aa	20.59	+	(14.16)
ad	-1.51		(8.01)
dd	-119.66	+	(81.84)
e	25.63	**	(2.57)
ae	-0.23		(7.99)
de	-4.68		(22.21)
aae	-0.13		(14.16)
ade	6.28		(8.01)
dde	-15.18		(81.84)
	Germination Maturity		
m	93.34	**	(5.42)
a	39.27	*	(16.35)
d	-104.58	*	(46.13)
aa	49.59	(*)	(28.69)
ad	20.69	+	(16.37)
dd	-387.14	*	(166.97)
e	28.52	**	(5.42)
ae	-0.33		(16.35)
de	-17.67		(46.13)
aae	2.77		(28.69)
ade	5.79		(16.37)
dde	-39.78		(166.97)

** significant at the 1 % probability level;
* significant at the 5 % probability level;
(*) significant at the 10 % probability level;
\+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

Cross 3 exhibited significant effects of the mean, environmental effect and the additive effect for median germination (T50SG). Both the environmental effect and additive effect were positive. The germination maturity (T90SG) in this cross appeared to be directed by the mean, the environmental effect, additive genetic effect, dominance effect, additive x additive and dominance x dominance epistasis. The dominance and dominance x dominance effects were negative while all other effects were positive. The cool environment prolonged median germination and germination maturity 26 and 29 days from the background means.

VII.5) Dry Weight Maturity and Grain Colour Maturity

The parameters estimated by the generation mean analysis for times to dry weight maturity and grain colour maturity are presented in Table 44.

Table 44. Estimation of the components of generation means on a twelve-parameter model for times to dry weight maturity (T90DW) and grain colour maturity (T90COL) in the three wheat crosses.

Gene effects	Cross 1 Estimates	s.e.	Cross 2 Estimates	s.e.	Cross 3 Estimates	s.e.
			Dry Weight Maturity			
m	43.26 **	(4.06)	40.85 **	(5.41)	48.96 **	(4.32)
a	-31.70 *	(12.58)	-19.16 +	(14.20)	5.46	(10.18)
d	-22.93	(35.02)	-14.10	(43.12)	17.92	(32.98)
aa	13.14	(25.16)	19.32	(27.86)	-11.44	(18.36)
ad	-33.27 *	(12.64)	-14.75 +	(14.42)	6.09	(10.41)
dd	-93.32	(137.06)	-89.06	(154.94)	58.80	(107.67)
e	7.87 (*)	(4.06)	11.82 *	(5.41)	18.88 **	(4.32)
ae	1.88	(12.58)	-12.76	(14.20)	-0.09	(10.18)
de	-35.49 +	(35.02)	-4.96	(43.12)	-2.41	(32.98)
aae	14.54	(25.16)	8.52	(27.86)	-0.98	(18.36)
ade	4.87	(12.64)	-11.22	(14.42)	-1.90	(10.41)
dde	-104.84	(137.06)	-25.74	(154.94)	-19.48	(107.67)
			Grain Colour Maturity			
m	46.49 **	(2.19)	55.36 **	(2.28)	47.01 **	(4.94)
a	6.89 +	(5.26)	6.58	(7.15)	-0.40	(8.32)
d	-2.44	(16.85)	98.67 **	(19.81)	14.00	(33.99)
aa	6.95	(10.04)	-31.66 *	(12.51)	-35.40 *	(14.24)
ad	6.86 +	(5.35)	3.76	(7.16)	-1.38	(8.56)
dd	-27.54	(57.04)	312.04 **	(72.75)	153.04 +	(90.26)
e	14.76 **	(2.19)	16.25 **	(2.28)	14.48 **	(4.94)
ae	4.67	(5.26)	6.55	(7.15)	1.67	(8.32)
de	-1.77	(16.85)	8.04	(19.81)	-24.91	(33.99)
aae	4.29	(10.04)	-9.04	(12.51)	36.70 *	(14.24)
ade	5.16	(5.35)	9.75 +	(7.16)	2.17	(8.56)
dde	-24.34	(57.04)	51.28	(72.75)	-217.48 *	(90.26)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

There was no significant generation effects in analysis of variance for dry weight maturity (T90DW) in all the three crosses (Table 1,4 and 7).

The means and the environmental effects were significant in all crosses. The cool environment increased time to dry weight maturity between 8 to 19 days to the background means. Cross 1 showed equivocally significant additive and additive x dominance effects, both effects were negative.

Grain colour maturity (T90COL) was a function of genetic effects in cross 2 (Tordo x Gabo). In this cross the dominance effect, additive x additive and dominance x dominance effects were significant. The effect of dominance and dominance x dominance were positive, while the additive x additive effect was negative. Since the dominance and dominance x dominance epistasis are the components of the heterozygous genotypes, it could be predicted that the hybrid from this cross will have very late grain colour maturity. In the third cross the genetic effects which were equivocally significant were additive x additive, additive x additive x environment and dominance x dominance x environment. The dominance x dominance x environment interaction was very large in magnitude and was negative. The additive x additive epistasis was negative and similar in magnitude to cross 2.

VII.6) Germinations at Harvest Ripeness

The results of generation mean analysis for standard germination and potential germination at harvest ripeness are presented in Table 45. The generation means corresponding to these analyses are presented in Tables 11, 13 and 15.

Table 45. Estimation of the components of generation means on a twelve-parameter model for standard germination and potential germination at harvest ripeness in the three wheat crosses.

Gene effects	Cross 1 Estimates		s.e.	Cross 2 Estimates		s.e.	Cross 3 Estimates		s.e.
				Standard Germination at HR					
m	5.28	*	(1.91)	17.93	*	(8.35)	7.45		(7.49)
a	6.20	+	(4.46)	3.00		(20.92)	-5.63		(17.05)
d	0.62		(14.52)	63.96		(65.27)	-23.69		(56.39)
aa	-44.14	**	(8.70)	-9.86		(36.26)	12.03		(30.00)
ad	5.84	+	(4.54)	-6.89		(21.12)	-19.35	+	(17.74)
dd	158.88	**	(49.04)	148.64		(215.75)	-66.06		(179.05)
e	5.28	*	(1.91)	-0.50		(8.35)	2.26		(7.49)
ae	-8.74	(*)	(4.46)	7.64		(20.92)	-11.47		(17.05)
de	39.79	*	(14.52)	-6.41		(65.27)	23.52		(56.39)
aae	-35.94	**	(8.70)	-2.70		(36.26)	-3.65		(30.00)
ade	-9.11	(*)	(4.54)	-1.16		(21.12)	-22.04	+	(17.74)
dde	204.36	**	(49.04)	27.32		(215.75)	90.78		(179.05)
				Potential Germination at HR					
m	15.25	*	(6.44)	25.63	**	(6.06)	37.86	**	(8.52)
a	47.05	*	(21.18)	25.60	+	(16.96)	35.30	+	(22.62)
d	-100.72	(*)	(57.34)	-30.92		(49.73)	13.17		(68.27)
aa	-25.67		(37.59)	-20.53		(31.07)	-22.54		(44.16)
ad	36.34	+	(21.22)	10.96		(17.15)	9.06		(23.15)
dd	-113.36		(216.33)	-12.22		(177.88)	72.82		(246.04)
e	7.69	+	(6.44)	0.90		(6.06)	24.50	**	(8.52)
ae	-12.34		(21.18)	30.61	(*)	(16.96)	23.40	+	(22.62)
de	11.93		(57.34)	-90.74	(*)	(49.73)	134.56	(*)	(68.27)
aae	-55.11	+	(37.59)	26.73		(31.07)	-68.52	+	(44.16)
ade	-22.19	+	(21.22)	13.88		(17.15)	6.09		(23.15)
dde	249.40	+	(216.33)	-236.46	+	(177.88)	511.66	(*)	(246.04)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

Only cross 1, Tordo x Karamu, showed a significant generation x environment interaction in the combined analysis of variance for standard germination at harvest ripeness. Apart from the significant effect of the mean (*m*) and the environmental effect, *aa* and *dd* epistasis were both significant. The magnitude of *dd* epistasis was relatively large and positive, while the *aa* epistasis was relatively smaller and negative. The interaction of genetic effects with environmental effect were all significant (i.e. *ae, de, aae, ade* and *dde*) with *dde* being relatively large in magnitude.

Dominance x dominance type epistasis increased the mean of all generations included in the analysis except for F_2, while the additive x additive type of epistasis decreased the values of both parents and backcross selfed generations. The *aae* effect was negative so it had a decreasing effect in the higher value environment (cool environment for this character). The *dde* effect was positive so it has enhancing effect in the cool environment and had diminishing effect in the warm environment. The effect of environment was equivocally significant, despite the nonsignificant environment effect in the analysis of variance.

There were no significant generation effects, environmental effects nor generation x environment interaction effects in the analysis of variance for standard germination at harvest ripeness in cross 2 and cross 3. As the parents in each of the two crosses are putatively different in preharvest sprouting resistance, the non significant generation effect in these two crosses could be attributed to the high standard errors of this character rather than the lack of genetic control or the resemblance between the two parents in the cross. The generation mean analyses did not reveal any significant effect in cross 3, and only the mean effect was significant in cross 2 (Coefficients of Variation for this character equal 106.78 and 129.42 % for cross 2 and cross 3 respectively).

There were significant generation x environment interactions in cross 2 and cross 3 for potential germination at harvest ripeness. In cross 2 (Tordo x Gabo) the significant effects detected by generation

mean analysis were the mean (m), additive x environment effect and dominance x environment effect. The *ae* effect has an increasing effect on the higher mean parent and the backcross selfed to this parent in the higher mean environment (warm environment). The effect (ae effect) was reversed in the other environment (i.e. it decreased the mean of the parent with the higher mean value and the backcross selfed to this parent). The dominance x environment effect was negative, this resulted in the net increase in the expected value of all generations in the test, except for F_2, in the environment with the higher mean (warm environment for this character). The environmental effect has no significant contribution to the expected values of the generation means for this character.

For cross 3 (Tordo x Sonora 64A) the effects which were significant included the mean effect, the environmental, dominance x environment and the *dde* interaction effects. The later two effects were significant at the 10 % probability level but their magnitudes were relatively large.

The generation mean analysis for potential germination at harvest ripeness of cross 1 showed an equivocal significant additive effect and a negative dominance effect.

VII.7) Grain Dry Weight

The parameters estimated for grain dry weight at harvest ripeness and for the maximum grain dry weight of the three wheat crosses are presented in Table 46. The generation means corresponding to the analyses are presented in Tables 17, 19 and 21.

Table 46. Estimation of the components of generation means on a twelve-parameter model for grain dry weight at harvest ripeness and maximum grain dry weight in the three wheat crosses.

Gene effects	Cross 1 Estimates	s.e.	Cross 2 Estimates	s.e.	Cross 3 Estimates	s.e.
			Grain Dry Weight at Harvest Ripeness			
m	48.78 **	(1.23)	50.83 **	(1.30)	50.76 **	(1.35)
a	-4.68 +	(2.99)	-1.35	(3.24)	-1.96	(3.80)
d	-4.47	(9.47)	2.77	(10.15)	13.80 +	(11.12)
aa	1.49	(5.87)	-1.50	(5.61)	-9.24 +	(6.53)
ad	-5.38 (*)	(3.02)	-3.03	(3.37)	-3.76	(3.82)
dd	-15.35	(32.80)	12.22	(33.47)	63.96 +	(38.62)
e	7.01 **	(1.23)	4.26 **	(1.30)	7.35 **	(1.35)
ae	-4.46 +	(2.99)	1.25	(3.24)	-3.61	(3.80)
de	3.54	(9.47)	-4.15	(10.15)	-2.38	(11.12)
aae	11.75 (*)	(5.87)	-2.92	(5.61)	2.27	(6.53)
ade	-4.17 +	(3.02)	-0.50	(3.37)	-2.32	(3.82)
dde	-43.26 +	(32.80)	7.17	(33.47)	-14.15	(38.62)
			Maximum Grain Dry Weight			
m	51.91 **	(0.99)	51.98 **	(1.77)	53.51 **	(1.43)
a	-12.54 **	(3.20)	-5.91 +	(4.65)	-0.66	(4.00)
d	-2.65	(8.73)	-3.12	(14.14)	16.53 +	(11.71)
aa	5.20	(6.42)	3.46	(9.10)	-10.69 +	(6.89)
ad	-13.56 **	(3.20)	-6.57 +	(4.74)	-2.39	(4.01)
dd	-32.99	(34.83)	-17.03	(50.69)	69.03 +	(40.70)
e	4.75 **	(0.99)	3.85 *	(1.77)	8.23 **	(1.43)
ae	-2.61	(3.20)	-1.63	(4.65)	-2.91	(4.00)
de	-9.48 +	(8.73)	-9.13	(14.14)	-4.23	(11.71)
aae	13.32 (*)	(6.42)	0.08	(9.10)	3.51	(6.89)
ade	-1.53	(3.20)	-3.10	(4.74)	-1.99	(4.01)
dde	-64.93 (*)	(34.83)	-10.46	(50.69)	-25.17	(40.70)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

In all the three crosses there were no significant differences among generations for grain dry weight at harvest ripeness but the environmental effects were significant in all three crosses. The generation mean analysis of all the three crosses showed that the only two important effects which significantly influence the grain dry weight at harvest ripeness were the means and the environmental effects. The cool environment added between 4.26 mg/grain to 7.35 mg/grain to the background mean dry weight at harvest ripeness.

There was significant generation x environment interaction for maximum grain dry weight in cross 1. In this cross the generation mean analysis showed a highly significant additive effect and additive x dominance effect, apart from the mean effect and the environmental effect. The *aae* effect and *dde* effect were also significant at the 10 % probability level. Many of these effects, i.e. *a ad* and *dde* were negative. The additive effect for this character in cross 1 is negative as in cross 2 and cross 3 in spite of the larger mean of P_1 (Tordo acts as P_2 in crosses 1 and 2 and acts as P_1 in cross 3 for this character). This may imply that the additive effect results in smaller grains.

The environmental effects were also significant in cross 2 and cross 3. The cool environment added 4.8, 3.9 and 8.2 mg/grain to the background mean in crosses 1, 2 and 3 respectively.

VII.8) Base α-Amylases

The parameters estimated from the generation mean analysis for the characters base α-amylase at harvest ripeness and base α-amylase at embryo maturity in the three wheat crosses are presented in Table 47. The corresponding generation means used in the analysis are presented in Tables 23, 27 and 31.

Table 47. Estimation of the components of generation means on a twelve-parameter model for base α-amylases at harvest ripeness and at embryo maturity in the three wheat crosses.

Gene effects	Cross 1 Estimates	s.e.	Cross 2 Estimates	s.e.	Cross 3 Estimates	s.e.
			Base α-Amylase at HR			
m	3.3554 **	(0.0881)	3.9154 **	(0.2295)	3.4332 **	(0.1411)
a	0.1921	(0.1978)	0.2580	(0.6138)	0.1799	(0.2826)
d	0.3701	(0.6600)	2.8973 +	(1.8446)	0.2418	(1.0180)
aa	-0.5383 +	(0.3716)	-1.4935 +	(1.0754)	-0.2824	(0.5203)
ad	0.1327	(0.2010)	-0.8249 +	(0.6161)	0.1322	(0.2940)
dd	2.5930 +	(2.1425)	12.4284 (*)	(6.3223)	0.8776	(3.0781)
e	-0.0240	(0.0881)	0.6440 *	(0.2295)	0.1391	(0.1411)
ae	0.2977 +	(0.1978)	0.2022	(0.6138)	0.1381	(0.2826)
de	-0.1968	(0.6600)	2.1312 +	(1.8446)	0.0392	(1.0180)
aae	0.2193	(0.3716)	0.0919	(1.0754)	0.0358	(0.5203)
ade	0.3995 (*)	(0.2010)	-0.3522	(0.6161)	0.2416	(0.2940)
dde	-1.1302	(2.1425)	4.0312	(6.3223)	-0.4288	(3.0781)
			Base α-Amylase at Embryo Maturity			
m	no estimates		4.2287 **	(0.9218)	3.1579 **	(0.3942)
a	for cross 1		-4.1655 (*)	(2.3217)	-0.2245	(0.9006)
d			-0.3204	(7.2216)	2.2242	(2.9729)
aa			-0.0408	(4.5782)	-0.4158	(1.5357)
ad			-5.8302 *	(2.3521)	-0.9450 +	(0.9151)
dd			0.1078	(25.4799)	11.3151 +	(9.3140)
e			0.4626	(0.9218)	0.1493	(0.3942)
ae			1.4151	(2.3217)	-2.3093 *	(0.9006)
de			0.3382	(7.2216)	2.3410	(2.9729)
aae			0.9700	(4.5782)	-0.1212	(1.5357)
ade			1.8157	(2.3521)	-3.6825 **	(0.9151)
dde			-2.8862	(25.4799)	9.2178	(9.3140)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

Cross 2 (Tordo x Gabo) showed significant differences among generations as well as generation x environment interaction for base α-amylase at harvest ripeness. Other than the mean and the environment effect, only the dominance x dominance epistasis effect was significant at the 10 % probability level. The parameters estimated which were greater than their standard errors were *d*, aa, a*d* and *d*e effects. For this cross the warm environment increased the base α-amylase at harvest ripeness by 0.6440 mEU/g (in log scale). The dominance gene effect and the dominance x dominance epistasis are both positive, indicating that the heterozygous genotype, such as a hybrid F_1, will have a high value of base amylase at harvest ripeness. Therefore this results would argue against the production of hybrids to improve resistance to sprouting damage.

Neither cross 1 nor cross 3 showed significant generation effects in the analysis of variance. However the generation mean analysis of cross 1 showed equivocal significant additive x dominance x environment effects at the 10 % probability level.

For base α-amylase at embryo maturity, cross 3 showed significant generation x environment interaction effects while cross 2 showed significant generation effects. The generation mean analysis showed highly significant mean effects in both crosses, but neither of the two crosses showed significant environmental effects (e). In cross 2 significant genetic effects were additive effects and additive x dominance effects; both are negative. Cross 3 had ae and a*d*e as significant genetic effects and both effects were negative. The negative a*d*e effect resulted in an increasing value of the higher parent and the backcross selfed to this parent in the environment with higher mean, on the other hand it decreased the value of the lower parent and the backcross selfed to this parent in the same environment.

VII.9) Germinative α-Amylase at Embryo Maturity

The parameters estimated from generation mean analysis for germinative α-amylase at embryo maturity are presented in Table 48. The corresponding generation means used in the analysis are presented in Tables 27 and 31. There was no estimation for this character in cross 1 because of incomplete set of generation means.

Table 48. Estimation of the components of generation means on a twelve-parameter model for germinative α-amylase at embryo maturity in the two wheat crosses.

Gene effects	Cross 2 Estimates	s.e.	Cross 3 Estimates	s.e.
	Germinative α-Amylase at Embryo Maturity			
m	6.6729 **	(1.2081)	4.7599 **	(1.3094)
a	-3.9045 +	(3.3177)	1.1456	(1.8490)
d	9.6836	(9.8269)	-2.5627	(8.6834)
aa	-8.0206 +	(5.8262)	-1.0361	(3.0853)
ad	-4.5330 +	(3.3418)	0.5008	(1.9797)
dd	45.1821 +	(34.1425)	-4.3388	(20.7079)
e	0.7420	(1.2081)	0.2003	(1.3094)
ae	-0.0330	(3.3177)	1.1234	(1.8490)
de	8.4354	(9.8269)	0.7922	(8.6834)
aae	-7.2928 +	(5.8262)	3.2587 +	(3.0853)
ade	0.1635	(3.3418)	2.5225 +	(1.9797)
dde	43.3720 +	(34.1425)	-9.0744	(20.7079)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

For germinative α-amylase at embryo maturity, cross 2 and cross 3 did not show significant differences among generations in the analyses of variance nor was there any significant generation x environment interaction. In these two crosses only the mean effect was significant. The environmental effects in these two crosses were not significant.

VII.10) GA3 α-Amylases

The parameters estimated from the generation mean analysis for GA3 α-amylase at harvest ripeness and at embryo maturity are presented in Table 49. The generation means corresponding to the analysis are presented in Tables 23, 27 and 31.

Table 49. Estimation of the components of generation means on a twelve-parameter model for GA_3 α-amylase at harvest ripeness and at embryo maturity in the three wheat crosses.

Gene effects	Cross 1 Estimates	s.e.	Cross 2 Estimates	s.e.	Cross 3 Estimates	s.e.
			GA3 α-Amylase at HR			
m	3.7642 **	(0.2068)	5.0873 **	(0.2718)	4.9003 **	(0.3970)
a	0.7388 +	(0.5801)	1.6859 *	(0.7815)	-0.3763	(0.9269)
d	-3.1506 (*)	(1.6986)	0.5048	(2.2590)	-1.9075	(3.0185)
aa	-0.0789	(1.0027)	-3.0832 (*)	(1.5586)	-0.7050	(1.6206)
ad	0.5029	(0.5814)	0.2975	(0.7870)	-1.4060 +	(0.9423)
dd	-6.4482 +	(5.9149)	10.6790 +	(8.5416)	-3.8006	(9.6697)
e	0.3256 +	(0.2068)	0.4565 +	(0.2718)	0.5396 +	(0.3970)
ae	-0.3653	(0.5801)	0.0581	(0.7815)	0.1781	(0.9269)
de	-1.9965 +	(1.6986)	-1.7326	(2.2590)	0.6445	(3.0185)
aae	0.9811	(1.0027)	0.0644	(1.5586)	-0.6532	(1.6206)
ade	-0.6437 +	(0.5814)	-0.7048	(0.7870)	-0.3811	(0.9423)
dde	-7.2186 +	(5.9149)	-3.9150	(8.5416)	4.3710	(9.6697)
			GA3 α-Amylase at Embryo Maturity			
m	no estimates		7.0308 **	(0.6363)	6.2473 **	(0.7848)
a	for cross 1		-3.1027 +	(1.8419)	4.1166 (*)	(2.1422)
d			2.9002	(5.3052)	-0.7836	(6.3663)
aa			-1.4537	(3.4108)	-2.7125	(4.1232)
ad			-4.0541 *	(1.8543)	4.0979 (*)	(2.1739)
dd			3.0100	(19.3684)	9.0093	(23.0746)
e			-0.3581	(0.6363)	0.4664	(0.7848)
ae			1.7474	(1.8419)	-3.3602 +	(2.1422)
de			-5.5806 +	(5.3052)	-6.6094 +	(6.3663)
aae			1.4971	(3.4108)	6.1947 (*)	(4.1232)
ade			0.6946	(1.8543)	-3.3986 +	(2.1739)
dde			-13.3192	(19.3684)	-40.7096 (*)	(23.0746)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level;
+ Estimate larger than its standard error.
Values in parentheses are standard errors of the estimates.

Of the three crosses only cross 2 and cross 3 showed significant generation effects in the analyses of variance for GA3 α-amylase at harvest ripeness. Cross 2 also showed a significant generation x environment interaction. The significant effects found in this cross were the mean, additive effect and additive x additive effect. The additive x additive effect was larger than the additive effect and was negative. Cross 1 showed a significant mean effect and an equivocal significant dominance effect. In cross 3, only the mean effect was significant. The environmental effect, like in the first two crosses, had the value larger than their standard error. The additive x dominance effect of this cross also had a value larger than its standard error.

For GA α-amylase at embryo maturity, cross 2 had significant generation x environment interaction. This cross showed significant effects of the mean and additive x dominance effect. In this cross the additive effects was negative despite the higher value of P_1 (Gabo = P_1 for this character). This suggested that the net additive effect had a diminishing effect on GA α-amylase at embryo maturity. Also the additive x dominance effect of cross 2 was negative.

The third cross (Tordo x Sonora 64A) had a significant mean effect. The genetic effect and the interactions which were equivocally significant were ae, a*de* and *dde*.

VII.11) Percent Sterility

The parameters estimated from generation mean analysis for percent sterility of the three wheat crosses are presented in Table 50. The corresponding generation means used in the analysis are presented in Table 37.

Table 50. Estimation of the components of generation means on a twelve-parameter model for percent sterility in the three wheat crosses.

Gene effects	Cross 1 Estimates	s.e.	Cross 2 Estimates	s.e.	Cross 3 Estimates	s.e.
			Percent Sterility			
m	4.74 **	(1.13)	12.19 **	(2.13)	6.25 **	(2.04)
a	16.53 **	(4.02)	-19.90 **	(6.20)	7.54 +	(5.96)
d	-31.13 **	(10.51)	-9.05	(17.82)	-24.93 +	(17.07)
aa	0.02	(7.20)	15.77 +	(12.48)	-1.66	(10.37)
ad	13.99 **	(4.03)	-23.03 **	(6.22)	3.45	(5.99)
dd	-50.70 +	(41.10)	-86.20 +	(68.04)	-42.46	(60.79)
e	1.06	(1.13)	8.71 **	(2.13)	-0.03	(2.04)
ae	1.74	(4.02)	-7.98 +	(6.20)	3.41	(5.96)
de	-1.82	(10.51)	24.82 +	(17.82)	-10.36	(17.07)
aae	5.24	(7.20)	0.05	(12.48)	-3.10	(10.37)
ade	0.39	(4.03)	-10.38 +	(6.22)	2.35	(5.99)
dde	-13.42	(41.10)	34.72	(68.04)	0.98	(60.79)

** significant at the 1 % probability level; * significant at the 5 % probability level; (*) significant at the 10 % probability level; + Estimate larger than its standard error. Values in parentheses are standard errors of the estimates.

The analysis of variances exhibited significant differences among generations in cross 1 for percent sterility of the spikelets. The significant generation x environment effects were detected in cross 1 and cross 3. Analysis of generation means showed that sterility percentage in cross 1 was controlled by the mean, additive, dominance and additive x dominance effects.

Cross 2 showed significant mean and environmental effects. Two genetic effects were equivocally significant despite the nonsignificant generation effect in this cross. The two effects were

additive and additive x dominance effects, both were negative. The third cross (Tordo x Sonora 64A) showed only a significant mean effect. The two parameters estimated which the values larger than their standard errors were additive and dominance effects.

CHAPTER 5

DISCUSSION

I) GENERAL DISCUSSION

I.1) Grain Maturity

In these experiments the maturity of the wheat grain has been evaluated from six different aspects.

(i) Maturity in relation to grain moisture content, called harvest ripeness, which has been defined earlier as the time when the grain reaches 12.5 percent moisture content.

(ii) Maturity in relation to the accumulation of grain dry weight which was defined as the time when grains reached 90 % of their maximum dry weight. This variable is close to the conventional estimation of "physiological" maturity.

(iii) Maturity in relation to the build up of pigment in the testa, which was measured as the time when the grains reached 90 % of their maximum colour.

(iv) Maturity in relation to the development of the embryo (embryo maturity) which was indirectly expressed by the time when the grains acquired 90 % potential germination with dormancy broken.

(v) Maturity in relation to the readiness of the aleurone layer to synthesize α-amylase under standard germination conditions. This maturity is referred to as amylase maturity.

(vi) Maturity as in (v) but with the germination imbibant being a gibberellic acid solution (1×10^{-5} M or 1×10^{-1} M), called GA amylase maturity. This maturity reflects onset of the competency of the aleurone tissue to respond to GA.

Among the six maturity-parameters, dry weight maturity and grain coat maturity were the earliest events. The synchrony between the two parameters is in agreement with the observation of Hanft and Wych (1982) who note that complete loss of the green colour from the kernel occurs close to physiological maturity.

Harvest ripeness occurred later than dry weight maturity and grain colour maturity. In these experiments the timing of harvest ripeness of different cultivars was not significantly different within either of the two environments, although it was considerably delayed in cool conditions (Table 1,4 and 7).

The two amylase maturities occurred at approximately the same time as harvest ripeness, while embryo maturity was the latest event. This juxtaposition of the events suggested that the overall germination processes of the grains may require a fully developed embryo to trigger the aleurone to produce germinative enzymes. In other words, embryo maturity was the last component to be acquired before the grains were able to germinate. The interval between dry weight maturity and embryo maturity was quite long (45, 63 and 44 days in crosses 1, 2 and 3 respectively). This period was much longer than the time needed to accumulate another 10 percent of grain dry weight and thus must involve more subtle developmental changes than simply growth in mass.

It is likely that the germinative development of the embryo after amylase maturities may involve either a change in hormone levels in the embryo or an increase in sensitivity of target-tissue to the hormonal signal. This change is what was expected to occur during after-ripening. The most widespread change displayed by seeds during this period is the gradual reduction in dormancy (Bewley and Black, 1982). In wheat, the relevant process was postulated to be the decreasing of an inhibitor level from the pericarp (Miyamoto *et al.*, 1961), or the increase in sensitivity to gibberellic acid (Trewavas and Cleland, 1983). Other processes which has been speculated included dehydration of the grain (Michell *et al.* ,1980),increasing of the oxygen permeability of the grain coat (Belderok, 1968).

I.2) Germinability

The two germination tests at harvest ripeness (standard and potential germinations), determine whether the generations are resistant or susceptible to sprouting damage, from the embryo sprouting point of view. The susceptible cultivar or generation would have a high level of germination at harvest ripeness. Among the four cultivars used as parents in the three crosses, Tordo consistently showed low standard germination and potential germination at harvest ripeness in both environments. Karamu showed low germination percentage at harvest ripeness, but showed a moderate level of potential germination at this stage under the warm ripening environment. The F_2 and F_3 generations of the cross Tordo x Karamu showed higher levels of standard germination at harvest ripeness under the warm ripening environment compared to the two parents. These segregating generations must have transgressive segregation under the warm environment for this character. In the cool ripening environment the F_2 generation did not have a higher mean standard germination at harvest ripeness compared to the two parents.

Gabo showed a high level of germination at harvest ripeness under the warm ripening environment but not under the cool ripening environment. The F_2 generation of this cross had an intermediate level of germination between the two parents in the warm ripening environment. In the cool ripening environment the F_2 generation showed transgressive segregation in potential germination. The level of potential germination of the F_2 exceeded both parents in this environment.

Sonora 64A showed a high level of germination at harvest ripeness when grain development was in the warm ripening environment, but in the cool environment its germination percentage was quite low. The F_2 generation of the cross Tordo x Sonora 64A had an intermediate level of germination in the warm ripening environment.

Median germination or median embryo maturity when related to harvest ripeness are good indicators of germinability of the grains. Whenever median germination (or median embryo maturity) preceded the harvest ripeness the standard germination (or potential germination) at harvest ripeness was usually high. Even when harvest ripeness preceded median germination (or median embryo maturity) the level of germination percentages could be high if harvest ripeness and these times were close. The condition that ensured low levels of germination at harvest ripeness was when harvest ripeness occurred much earlier than median germination (or median embryo maturity) the difference in time being more than the interval between median germination (or median embryo maturity) and germination maturity (or embryo maturity). If this was the case, the germination percentage at harvest ripeness would be less than 10 % (because the germination curves were symmetrical).

I.3) Dormancy

Dormancy percentages obtained, provide an estimate of true dormancy excluding the immaturity of the embryo. The validity of this view does depend on whether the "special germination" method does truly break dormancy. The earlier work (Gordon, 1975; Cross, 1977; Very, 1978) does show that there is a real effect in breaking dormancy. However the population of wheat used in the present study consisted of different generations with different genetic structures from different crosses. The effect of special germination conditions did not always break dormancy. This posed a problem in calculating the dormancy. Dormancy is measured as the difference between potential germination and standard germination, as a ratio to the potential germination. If the former (potential germination) is zero , then no maturity is observed, and no valid statement can be made about dormancy under these conditions.

In the cool ripening environment, Tordo exhibited 100 percent and 17 percent dormancy in crosses 1 and 2 respectively. But the dormancy percentage of this cultivar in the warm ripening environment

in all the three crosses, and the dormancy under the cool ripening environment in cross 3 were undefined. The differences in dormancy percentages between cross 1 and cross 2 of Tordo could not be proved, since each estimate was derived from mean standard germination and mean potential germination under a particular environment. The generally low potential germination at harvest ripeness of Tordo indicated that at harvest ripeness the embryos were still immature. Karamu also showed a high level of dormancy at harvest ripeness under both the warm and cool ripening environments. The mean dormancy of the F_2 generation in the cross Tordo x Karamu was low under the warm ripening environment and fully dormant in the cool environment. This implied that the environmental effect was an important factor determining the levels of dormancy. However no combined analysis of variance or generation mean analysis were carried out for this character. Gabo showed a low level of dormancy at harvest ripeness in the warm ripening environment (38%) and no dormancy in the cool ripening environment. Sonora 64A expressed a moderate level of dormancy at harvest ripeness in both ripening environments (44 and 58 % in the warm and cool ripening environment).

The generations ripening under the warm environment expressed higher germinability. The present experiment supported the finding by Plett and Larter (1986) with wheat line RL4137 (a sprouting resistant wheat cultivar) that the higher the maturation temperature the higher the germination of the grain. There were reports by several workers (e.g. Cross, 1977; Briggle, 1980; Strand, 1989) that higher temperature and more intense radiation during the grain maturation period generally reduced seed dormancy.

I.4) Grain Weight at Harvest Ripeness and Maximum Grain Dry Weight

In most generation-environment combinations the grain dry weights at harvest ripeness were slightly lower than the maximum grain dry weights. This indicated that at harvest ripeness the grains had not yet reached their maximum grain dry weight.

Since harvest ripeness occurred after dry weight maturity (time of 90 % maximum dry weight) in all generations under both ripening environments, the harvest ripeness therefore, was a stage closer to the time when grain attained maximum grain dry weight more than the dry weight maturity (T90DW) in these experiments. This result was in agreement with the work of Gordon *et al.* (1979) who found that differences in dry weight of grains at different levels of grain moisture content were small (the three levels of moisture were 12.5, 17.5 and 20 %). These authors used Gompertz equation to describe the grain growth, and the result showed that at the grain moisture content between 20 % to 12.5 %, the grain dry weight was increasing. At 12.5 % the grain weights reached about 92-99 % of the upper asymptotes in the four wheat cultivars (Gordon *et al.*, 1979).

The estimation of occurrence of physiological maturity (time at which the grain first attained the "maximum" grain dry weight) from the grain growth pattern, has been investigated by others using different functions to explain the grain growth (e.g. Loss, *et al.*, 1989). The three functions used were linear, cubic and logistic. They reported that among the three functions, the logistic function was found to be the most appropriate model to describe grain growth. The time when "maximum" grain dry matter was achieved varied with the function fitted to the data.

Meredith and Jenkins (1970) defined ripeness for harvesting in New Zealand conditions as when the grains reach 16.7 % moisture content (20 % dry basis). Under field conditions they reported that some wheat cultivars approached a maximum dry weight at or after ripeness and some cultivars attained a maximum dry weight at ripeness beyond which there was loss of dry weight, with a subsequent recovery (Meredith and Jenkins, 1970). While Hanf and Wych (1982) observed that grain moisture at the times grains reach maximum grain dry weight varied from 13.4 to 28.1 percent, Clark (1983) reported that physiological maturity occurred at 32.4 to 43.6 % moisture content. It can be concluded that the attainment of maximum grain dry weight

may occur at a certain level of grain moisture depending on the environmental conditions in which the grains developed. As Hanft and Wych (1982) have pointed out, grain moisture content was too variable to be considered a reliable indicator of physiological maturity.

It is generally accepted that the grains which developed from the basal florets weighed more than the grains developed from the distal florets (Kirby,1974; Rawson and Evans,1970; Simmons and Moss, 1978; Simmons and Crookston, 1979). The difference in kernel weight has been attributed to the difference in kernel growth rate during the linear dry matter accumulation period, and the difference in the anthesis time among florets in the same spikelet (Simmons and Crookston ,1979). With this observation in mind the maximum grain dry weights in the present report are overestimates of the real average weight of grains. However, it serves the purpose for studying the basic pattern of development, and the environmental or genotype effects on grain maturation.

It was clear that cool environment yielded heavier grains than the warm environment for all cultivars. This result was similar to that of Cross (1977) with six wheat genotypes. He observed that all the six genotypes showed higher maximum grain weight under the cool ripening environment (18/12 °C) compared with a warm ripening environment (30/20 °C).

I.5) α-Amylase Levels

Base α-amylase levels at harvest ripeness were not significantly different among generations in cross 1 and cross 3, but there were significant differences among generations in both environments for cross 2. At embryo maturity the estimated base α-amylase of Tordo in the warm environment showed large variation from cross to cross and the value was abnormally high in the first cross. There were significant differences among generations for base α-amylase at embryo maturity in cross 2, and a significant difference among generations within the warm ripening environment in cross 3.

The correlation coefficients between base a-amylase and germinative α-amylase at embryo maturity in the three crosses were 0.86, 0.48 and 0.80, all highly significant (Tables 26,30 and 34). Gordon (1975) has reported that base amylase and germinative response a-amylase had medium low and negative correlations (simple and partial correlations). As these relations were the same irrespective of the grain colour of the genotypes, he contended that these two characters were independent. The present experiment showed that the correlations between the two amylases may be low or high at the harvest ripeness time depending on the genetic populations used. But the levels of the two amylases may in fact be the same once the grain has lost dormancy such as at the time of embryo maturity.

Germinative α-amylase and GA_3 α-amylase at embryo maturity are normally higher than the same type of α-amylase at harvest ripeness. Paired t-tests for differences between germinative α-amylase at the two stages showed that in all the three crosses germinative α-amylase at embryo maturity were significantly higher than the levels at harvest ripeness, also paired t-tests showed that GA α-amylase at embryo maturity was higher than the GA α-amylase level at harvest ripeness in all the three crosses (Table 25,29 and 33). Among the six α-amylase activities estimated, germinative α-amylase at harvest ripeness significantly correlated with standard germination and potential germination at harvest ripeness in all the three crosses (Tables 26, 30 and 34). Base α-amylase at harvest ripeness correlated with standard germination and potential germination at harvest ripeness only in cross 2 (Table 30). GA α-amylase at harvest ripeness correlated with standard germination at harvest ripeness in cross 2 and cross 3 and correlated with potential germination at harvest ripeness in all the three crosses. Base on the correlations between variables it seems that germinative α-amylase at harvest ripeness was the most consistent variable that correlated with germination. Nevertheless the correlation coefficient cannot be interpreted as the change in one variable caused by a change in another variable. Cross (1977) also reported that base α-amylase at

harvest ripeness provides no discernible pattern with which to distinguish cultivars into dormant or non-dormant, whereas the α-amylase response activity (germinative α-amylase) at harvest ripeness differed among cultivars when developed in the warm environment. However the magnitude of the correlation coefficients in the present experiments were only moderate (Table 26, 30 and 33). GA α-amylase at harvest ripeness correlated with potential germination at harvest ripeness quite often.

GA α-amylase at embryo maturity correlated with potential germination at harvest ripeness in cross 2.

The effect of 10^{-5} or 10^{-4} M GA_3 in stimulating the grain to produce more α-amylase was evident with the paired t-test results with all the actual measurements of α-amylase levels over the total length of sampling period. The GA_3 α-amylase levels were significantly higher than germinative α-amylase levels at the 1 % probability level in all the three crosses (t = 7.86, df = 333, for cross 1: t = 11.21, df = 317, for cross 2; and t = 10, df = 311, for cross 3)

I.6) Maximum Colour Score

The maximum colour score recorded in these experiments showed that when the white-grained wheat was crossed with red-grained wheat the F_2 generations had a mean maximum colour score at an intermediate level between the two parents irrespective of the environment in which the wheat was grown. It may be worthwhile to clarify that the mean colour score of the segregating generations was the weighted averages of the various expressions of grain colour. The weighting was the frequency of the grains in each score class. Thus, the grain colour score (as well as the maximum colour score) was treated as a quantitative character. In cross 2 in which both parents were white grain cultivars the measurement of colour score in this cross may reflect the reaction of the polyphenol oxidase enzyme rather than measuring the red pigment phlobaphene as was postulated by Gordon

(1975). So the generation differences may indicate the difference in the level of the polymerizing enzyme, which is probably low in both parents.

I.7) Sterility Percentage

In all three crosses, sterility percentages were higher under the warm ripening environment. This result was in agreement with the earlier reports by Wardlaw (1970) and Warrington *et al.* (1977) who reported the higher number of fertile floret and more grain set at low temperature. The sterility percentage measured in these experiments may be an under-estimate of the mean sterility of the whole ear, because only the middle portion of the ear was used in measurments. This sterility percentage excluded the innate sterility of some distal florets which may differ among different genotypes. Fisher (1973) has reported that some wheat cultivars derived from Norin 10 such as Sonora 64, Lerma Roja 66 and Yorkstar had greater apical dominance within individual spikelets and resulted in more fertile florets per spikelet. However this sterility percentage would be an appropriate measurement of sterility when comparing the effects of environments.

II) GENE EFFECTS

The generation mean analysis results of maximum grain dry weight and germinative α-amylase at HR (Table 29 and 30) has shown that the six parameter model and the twelve parameter model yield similar estimates of the first six parameters. This could be expected, since in both models the estimation of the parameters were obtained by solving the normal equations (perfect fitted solution). The extra information from the twelve parameter model reveals how the genes act under different environments, e. g. the direction of *ae* will tell instantly that the difference between the two inbreds will increase or decrease when the environmental means increase. A negative *ae* means

the difference will decrease as the environment changes in a positive direction (the environmental mean becomes higher). Another obvious advantage of the twelve parameter model was that the environmental effect can be tested at the same time as other parameters. Twice the e parameters is the difference between the two environmental means. The six parameter model ignored the environmental effect and genetic x environment interaction from the model, so it was less informative. The parameters estimated by this model (also the first six parameters of the twelve parameter model) were in fact averaged effects of the estimates when analysed for each single environment separately. The analysis of the generation means for each environment will only give information about the gene effects in that particular environment. To apply the results to other environments, one must assume that there is no genotype environment interaction, which is a condition seldom found for most of these plant characters. In fact, estimates in just one environment are potentially biased by confounding the gene effects with the interaction effects.

II.1) Gene Effects Controlling the Maximum Colour Score

Considering the grain colour score to be controlled by the well known red grain genes, cross 1 and cross 3 should involve the crossing of parents which differ in only one locus for the red grain gene. Tordo is one of the parents in both crosses and has no gene for grain redness. The other parents in the two crosses were Karamu with one gene for grain redness (J. M. McEwan, personal communication), and Sonora 64A also with one gene for grain redness (Jan and Qualset, 1976). Cross 2 is distinct from the other two crosses because it involved only white grained wheats (even though the generation effect showed that there were colour difference among generations). Because sodium hydroxide reacts with the pigment phlobaphene to produce the red- brown phorogenic acid (Miyamoto and Everson, 1958), Gordon (1975) assumed that the NaOH test indicated the present or absence of this pigment. He further demonstrated that white grained wheats may lack the polymerizing enzyme, but the precusor (flavanol) level was the same as that of red grained wheat, he therefore proposed that the gene

for grain redness was possibly the gene for polyphenol oxidase (the polymerizing enzyme). In this cross in particular, the interpretation of the genetic effects would be more appropriate, if the gene being investigated is considered to be different from genes for grain redness. This line of thinking also applies to cross 1 and cross 3 when the epistasis effects were important, since it would be difficult to conceive the concept of epistasis in the populations which derived from the cross with only one gene segregating. In other words, these results suggest that there are genes other than the classical "red" genes which react under the NaOH test for phlobaphene (the putative grain coat pigment).

There were significant dominance, additive x additive and dominance x dominance gene effects for maximum colour score in cross 2. The additive gene effect was larger than its standard error but was not significant. Cross 3 showed significant additive x additive, additive x dominance and dominance x dominance epistasis effects. The environmental effect was significant at the 10 % probability level. Also there were significant *de*, *aae* and *dde* interaction effects. These results suggested that the gene effect controlling the grain coat colour did not only act additively, as has been believed, but is also affected by the interaction of genes between loci and interaction of genes with the environment.

One point to mention here is the similarity of the gene actions for maximum colour score and grain colour maturity in all three crosses. The environmental effects were significant more often for grain colour maturity, but for the maximum colour score the environmental effect was less important (only significant at the 10 % probability level in cross 3). These results suggested that genes controlling grain coat colour may also affect the time of grain colour maturity and that the latter character was influenced more by the environment than the former one.

The results of generation mean analyis of colour score in this study was not parallel with the expectation based on the segregation of single gene for grain redness. The mean colour score of the F_2

generation was the average score from different colour classes. The size of sample was probably not large enough to cover the different classes in the right proportions. This problem also occurred with other segregating generations. If the red grain gene segregated on only one locus and red was completely dominant to white, the colour score of F_2 generation would be expected to be $(P_2 + 3\ P_1)/4$, when P_1 is the mean value of the parent with a red gene and P_2 is the mean value of the parent with no red gene. None of the F_2 means in all the three crosses have the observed values close to the expected values.

II.2) Gene Effects of the Grain Maturity Characters

Characters related to grain maturity which did not show significant generation effects or generation x environment interactions in all the three crosses were harvest ripeness and dry weight maturity. This may be attributable to the similarity of the two parents in each of the three crosses. These two characters were determined by the mean and environment effects only, in these results.

The gene actions for median germination and germination maturity showed significant additive effects, and negative dominance for both characters. The magnitude of dominance was about two times larger than additive effect for median germination and about 2.5 times larger than additive for germination maturity. Their negative values indicated that dominance effects resulted in early median germination and germination maturity. This result also disfavour the production of heterozygous genotypes (i.e. hybrids), since heterozygosity would result in early median germination and germination maturity. For these attributes, it was clear that selection for late median germination and late germination maturity would be the option. The selection for these characters may need serial samples for germination tests, however. Prolonging sampling until full germination was reached would also be important.

Amylase maturity in crosses 1 and 3 showed significant *aa* epistasis, this effect in cross 3 was equivocal. The additive and dominance effects were small compared to the *aa* epistasis. The breeding strategy to exploit the *aa* effect is to select for homozygous lines from a segregating population derived from a cross.

The significant *aa* effect for amylase maturity indicated that selection for late amylase maturity should be deferred until later generations when plant reached high level of homozygosity. The gene effect for GA amylase maturity in cross 3 showed a large magnitude of dominance in a negative direction, the estimates was larger than its standard error although it was not significant. The negative dominance effect indicated that heterozygosity would result in earlier GA amylase maturity. This nature of gene action is evidence against production of hybrid wheat resistant to preharvest sprouting.

The cross between Tordo and Karamu showed a significant effect of epistasis x environment for median embryo maturity which suggesting that the genetic system for this character in this cross was complicated and selection needs to be carry out in later generations under different environments. Cross 3 (Tordo x Sonora 64A) showed significant dominance effect for median embryo maturity. The effect resulted in a mean increase (later median embryo maturity).

Embryo maturity showed a significant *aae* effect in cross 1 and the effect was negative. The other two effects controlling this character in cross 1 which had values greater than standard errors were dominance and additive x additive effect. The gene effects for embryo maturity in cross 3 appeared to be additive, *ade* (significant at the 5 % probability level) and additive x dominance (significant at the 10 % probability level). It appeared that the gene actions for median embryo maturity and for embryo maturity in this cross were quite different.

Breeding for resistance to sprouting damage should seek late embryo maturity. This would need the special germination tests of serial samples during grain maturation until well past harvest

ripeness so that reliable estimates of embryo maturity can be obtained from the fitted function. The significance of epistatic gene effects (*ad* in cross 3) and significant epistasis x environment interaction (aae in cross 1 and a*de* in cross 3) indicate that selection for late embryo maturity must be deferred until later generations. The gene effects for this character showed that the gene action has tendency to be duplicate epistasis (the opposite sign of *d* and *dd* effect), which suggested that selection for this character would be difficult.

Cross Tordo x Gabo showed a large magnitude of dominance and *dd* epistasis. This suggested that the hybrid from this cross would have very late grain colour maturity.

II.3) Gene Effects Controlling Germination

The germinations at harvest ripeness appeared to be the character with complex gene effects. The cross Tordo x Karamu showed that nearly all epistasis and epistasis x environment were significant, while the additive and dominance effects were not. The relative large magnitude of *dd* epistasis and *dde* interaction effects suggested that the hybrid would have high germination percentage. Negative aa would decrease the standard germination at harvest ripeness.

Potential germination at harvest ripeness of cross 1 showed an equivocal significant additive effect and a significant dominance effect in the negative direction. Cross 2 exhibited significant ae and *de* effects, while cross 3 showed significant *de* and *dde* effects. The environment effect was significant only in cross 3. In this cross the magnitude of *dde* was quite large and positive, about four times larger than *de* effect.

The significant interaction between epistasis and environment ae and *de* (in cross 2) and *de* and *dde* (in cross 3) indicated that additive effect , dominance gene effect and dominance x dominance epistasis were sensitive to environmental changes. Under these type of gene actions selection would be effective only for a specific environment.

II.4) Gene Effects Controlling the Grain Weight Characters

Cross 1 showed an equivocal significant *ad* effect for grain dry weight at harvest ripeness. For maximum grain dry weight this cross showed significant additive, a*d*, *aae* and *dde* effects. It appeared that the additive effect was negative for this character, despite the higher value of P_1 in the model. Tordo is a dwarf cultivar derived Rht_3 (or Gai_3) gene from Tom Thumb (Flintham and Gale, 1980). The Rht_3 alleles resulted in smaller grain weight and increase in grain number per ear in the F_4 random lines compared with the lines carries rht_3 alleles (Flintham and Gale, 1980). The results from the present experiments showed that the Rht_3 gene in Tordo may have effects in decreasing grain size as was reported by Flintham and Gale (1980).

The effect of Rht_3 gene on spikelet number was small indicated that the increased in grain number was due to an increase in fertility of distal florets within the spikelet (Flintham and Gale, 1980). This confounding effect of grain number on the grain weight was also pointed out by Chojecki *et al.*(1986). They contended that the genetic analysis for grain weight based on the basal florets of central spikelets would have failed to detect the most pronounced effect of chromosome 1A on grain weight, which effects florets 2 and 3, and that the interference by the difference in grain number per ear make studying the genetic effects for grain weight alone unreliable.

The genetic system controlling grain dry weight is of group 3 as classified by Hayman (1960) where epistasis, additive and/or dominance are significant, with epistasis at least as important as the other modes of gene action.

The conclusion that can be made about the gene effect for maximum grain dry weight in cross 1 was that additive x dominance epistasis as well as *aae* and *dde* interaction was important in determining this character. The effects of the Rht_3 gene in Tordo showed a strong effect in reducing the grain dry weight, as found in these studies.

II.5) Gene Effects Controlling the α-Amylase Levels

Only cross 2 showed significant gene effects controlling base α-amylase at harvest ripeness. In this cross the *dd* effect was significant at the 10 % probability level.

Base α-amylase at embryo maturity exhibited significant *a* and *ad* in cross 2; significant *ae* and *ade* in cross 3. Cross 2 seems to have partial duplicate gene interaction ($d \approx [1/3]\ dd$) but both *d* and *dd* were not significant.

It appeared that the environmental effects were not significant for base α-amylase at embryo maturity for both crosses 2 and 3. This was in agreement with the analysis of variance of cross 3, but was in contradiction with analysis of variance in cross 2.

Germinative α-amylase at harvest ripeness appeared to be regulated mainly by additive x environment interaction (*ae* significant at 10 % probability). in cross 1. None of the gene effects in cross 2 and cross 3 were significant (Table 30). Germinative α-amylase at embryo maturity (Table 38) neither showed significant environment effects nor gene effects in both cross 2 and cross 3.

GA3 α-amylase at harvest ripeness had significant additive and additive x dominance gene effect in cross 2. Cross 1 showed equivocal significant dominance effect for this character.

The GA3 α-amylase level at embryo maturity showed significant additive x dominance in cross 2. This cross the additive gene effects was negative and higher than its standard error (Gabo being P_1 in this cross). This showed that low GA α-amylase at embryo maturity is a dominant expression over the high GA_3 α-amylase at embryo maturity. The present results supported the finding of Bhatt *et al.*(1976) who reported that low α-amylase synthesis was dominant over the high α-amylase synthesis. Cross 3 showed equivocal significant *ae*, *ade* and

*dd*e effects. This cross seems to have over or super duplicate gene action (-12 *d* ≈ *dd*), but both gene action *d* and *dd* were not significant.

II.6) Gene Effects Controlling the Sterility Percentage

Percent sterility appeared to be controlled by additive and dominance gene action and the additive x dominance epistasis in cross 1. Cross 2 showed equivocal additive, and additive x dominance gene effects, whereas cross 3 showed no significant gene effects.

Dominance gene effects were negative in all crosses (significant only in cross 1), which indicated that the hybrids produced from these crosses would have low sterility. This may be one aspect of yield improvement by producing hybrid wheat. The effect of Rht_3 gene in increasing the grain number per ear has already been discussed in section II.3. It is unlikely that the increase in number of distal grains was the cause of high sterility in the basal florets. According to Zee and O'Brien (1970) the basal florets are closer to the vascular bundle than distal ones, so they should have a better chance to develop into grains. In relation to grain yield, it must be pointed out that it is assumed that the percent sterility in the sampled portion of the ear represent the sterility of the ear as a whole. As for the grain dry weight, the effect of some genes which effect the third and the fourth florets in the spikelet may have been excluded from the analysis of this character (Chojecki *et al.*,1986).

CHAPTER 6

CONCLUSIONS AND FUTURE RESEARCH

The results from these experiments may be concluded as the followings.

1) Cool ripening environment delayed most maturation aspects of the grains, decreased the grain germinability, and increased maximum grain dry weight and decreased percent sterility.

2) The sequence of occurrences of maturation traits in general was that grain colour maturity and dry weight maturity were the earliest events,followed by amylase maturity and GA amylase maturity.

3) Harvest ripeness occurred close to amylase maturity and GA amylase maturity, this event happened just prior to the time to maximum grain dry weight.

4) Median germination, germination maturity generally occurred after harvest ripeness.

5) Dormancy percentages at harvest ripeness of Tordo was 100 % in cross 1 and was undefined in crosses 2 and 3. Karamu, Gabo and Sonora 64A have the estimated dormancy equal 95,28 and 45 percent.

6) Tordo generally showed low percentages standard and potential germination at harvest ripeness in both ripening environments. Standard germinations of Karamu were low in both ripening environments. The potential germination percentage of this cultivar is intermediate in the warm ripening environment and was low in the cool ripening environment. Gabo has intermediate standard germination and high potential germination at harvest ripeness. But the two germination percentages were low in the cool ripening environment. Sonora 64A showed intermediate standard germination percentage and high potential germination percentage at harvest ripeness in the cool ripening environment.

7) Cool ripening environment yielded the grains with lower germinative α-amylase and GA α-amylase at harvest ripeness in cross 1 and 3. In cross 2 only GA_3 α-amylase of grains developed in the cool ripening environment was lower than that of grains developed in the

warm environment. Environment has no effects on base α-amylase levels in cross 1, but in crosses 2 and 3 the warm ripening environment produced grains with higher level of base α-amylase at harvest ripeness

8) Germinative α-amylase levels at harvest ripeness consistently correlated with the standard and potential germinations at harvest ripeness in all the three crosses. GA_3 α-amylase levels at harvest ripeness correlated with potential germination at harvest ripeness in all the three crosses and correlated with standard germination at harvest ripeness in crosses 2 and 3. Base α-amylase at harvest ripeness correlated with the germination percentages only in cross 2.

9) The results of generation mean analysis based on the twelve parameter model, for different attributes may be summarized as follows:-

9.1) Gene action of the genes control amylase maturity in cross 1 was of additive x additive epistasis.

9.2) The dominance effect were the major gene action for median embryo maturity in cross 3 and grain colour maturity in cross 2. The dominance effects were positive suggesting the lateness in times to embryo maturity and grain colour maturity in the F_1 hybrid produced by this cross.

9.3) Epistasis x environment interactions were important for embryo maturity (*aae* in cross 1, *a,ad* and *ade* in cross 3).

9.4) The gene action for grain colour maturity in cross 2 were dominance, *aa* and *dd* gene effects.

9.4) Standard germination at harvest ripeness of cross 1 wheat was controlled by epistasis and epistasis x environment types of gene actions. The significant genetic effects for potential germination at harvest ripeness were *ae* (cross 2), *de* (crosses 2 and 3) and *dde* (cross 3).

9.5) Maximum grain dry weight was controlled by additive, additive x dominance, *aae* and *dde* effects in cross 1. The additive effects were negative in all crosses (only in cross 1 that the effect was significant and unequivocal). It was speculated that the Rht_3 gene of Tordo may have role in controlling the grain weight also.

9.6) The unequivocal significant gene effect for base α-amylase at harvest ripeness in cross 2 was dominance x dominance type gene actions. The dominance effect for this character in this cross also large compared to the additive effect. This suggested that hybrids produced from this cross would have high level of base α-amylase. Base α-amylase at embryo maturity showed unequivocal significant *ae* effect (cross 3) and *ade* effects (crosses 1 and 3).

9.7) Only cross 1 showed unequivocal significant *ae* effect for germinative α-amylase at harvest ripeness.

9.8) GA_3 α-amylase at harvest ripeness of wheat cross 2 was controlled by genes with additive x additive gene action. GA_3 α-amylase at embryo maturity showed *aae* type of gene action in cross 1 and *ae*, *ade* and *dde* type of gene action in cross 3.

9.9) Maximum colour score as a quantitative character showed dominance, additive x additive and dominance x dominance gene action in cross 2. The gene action for maximum colour score in cross 3 (Tordo x Sonora 64A) were *aa, ad, dd, de,aae* and *dde*. It was speculated that the classical red gene may interact with some other genes and resulted in epistasis gene action (It was also possible to look at epistasis effects controlling the maximum colour score as the interallelic interaction between the wild type, 'no colour', alleles).

9.10) The gene action for grain sterility appeared to be additive, dominance and additive x dominance in cross 1. The negative value of dominance effects suggested that the hybrid F_1 from this cross will have low percent sterility, which may contribute to high yiled.

Scope for Future Research

In the present experiments the genes controlling each character were studied. Most of the characters were statistics obtained from a fitted function. Precision in getting the estimates is one factor controlling the reliability of these results. Differences between generations were also crucial in interpreting the generation mean analysis results. When a generation difference was not detected, the

analysis may only reflect a biometrical parameters which lack the biological meanings. Also in the present generation mean analysis the test for goodness of fit by chi square was not possible because all the degrees of freedom were used to estimate parameters. With more generations included in the analysis, the test for goodness of fit will be possible and more reliable results will be obtained.

The appropriate transformation for each character is also worth investigating in the future research. Appropriate transformation of the data may turn an effect which probably be multiplicative in nature into the additive effect. Under a different scale of measurement the magnitude or the direction of gene actions may change.

The genetic analysis of the characters measured from grains was complicated in nature because of the difference in ploidy and genetic constituention of the different tissues in the grains. The triploid scale model as proposed by Gale (1976) for α-amylase activity is well worth investigating. This would be possible if more assumptions were imposed on the model such as no epistasis or no genotype x environment inter action. Another way to make the triploid model analysis possible is by increasing the numbers of generations included in the analysis.

The quantitative analysis of grain colour score may give more light into the action of gene for grain redness, if the two parents are different in all the three genes for grain redness.

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Appendix 1. The planting medium for the wheat plants in the generation advance in the glasshouse.

The medium contains:-

1) 50 litres sand,

2) 30 litres sieved peat,

3) 180 g Osmocote (14-6.1-11.6),

4) 240 g Dolomite,

5) 72 g micromix.

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Appendix 2. The North Carolina State University nutrient solution, used to feed the plants in the glasshouse and climate rooms.

CLIMATE LAB - N.C.S.U. PHYTOTRON NUTRIENT

2 ml A + 2 ml B/l water

grams/litre

	Molecular Wt. (g)	Conc.	Final Soln.	PPM	
Stock solution A:					
Ammonium nitrate				N	56.05
NH_4NO_3	80.02	80.05	.1601		
Calcium nitrate				Ca	54.06
$Ca(NO_3)_2 \times 4H_2O$	236.15	159.25	.3185	N	37.79
Sequestrene 330				Fe	5.96
10% DTPA Na Fe	468.20	29.8	.0596	Na	2.93
Stock solution B:					
Potassium phosphate				K	7.18
KH_2PO_4	136.08	12.5	.025	P	5.69
Potassium phosphate				K	4.94
K_2HPO_4	174.17	5.5	.011	P	1.96
Potassium nitrate				K	49.42
KNO_3	101.11	63.9	.1278	N	17.71
Magnesium sulfate				Mg	6.08
$MgSO_4 \times 7H_2O$	246.50	30.81	.06162	S	8.02
Sodium sulfate				Na	22.98
Na_2SO_4	142.05	35.5	.071	S	16.03
Zinc sulfate				Zn	0.011
$ZnSO_4 \times 7H_2O$	287.55	0.025	.00005	S	0.006
Manganese chloride				Mn	0.144
$MnCl_2$	197.92	0.26	.00052	Cl	0.186
Copper sulfate				Cu	0.005
$CuSO_4 \times 5H_2O$	249.68	0.01	.00002	S	0.003
Boric acid					
H_3BO_3	61.82	0.35	.0007	B	0.123
Sodium molybdate				Na	0.001
$Na_2MoO_4 \times 2H_2O$	241.93	0.0027	.0000054	Mo	0.002

Nutrient	PPM	µm	Nutrient	PPM	µm
N	111.55	NH_4 2200 NO_3 6130	B	0.123	BO_3 11.39
P	7.65	PO_4 6.8	Mn	0.144	2.55
K	61.54	80	Cu	0.005	0.08
S	24.06	SO_4 750	Zn	0.011	0.17
Ca	54.06	1280	Mo	0.002	0.02
Fe	5.96	125	Cl	0.186	5.36
Mg	6.08	250	Na	25.911	1125

pH of final solution = 6.5-7.5

Appendix 3.A. Planting dates and number of pots planted with the 6 generations of cross 1 wheat in PPD glasshouse before transferring to the controlled climate rooms*.

Date	Generations					
	P_1 (Tordo)	P_2 (Karamu)	F_2	F_3	$BC_1(P_1)S_1$	$BC_1(P_2)S_1$
	(no. of pots)					
8 March 1985	-	-	43	43	22	22
15 March 1985	-	-	86	86	44	44
22 March 1985	44	44	43	43	22	22
Total	44	44	172	172	88	88

* Plants were transferred into climate rooms on May 10th, 1985.

Appendix 3.B. Planting dates and number of pots planted to the 6 generations of cross 2 wheat in PPD glasshouse before transferring to the controlled climate rooms*.

Date	Generations					
	P_1 (Tordo)	P_2 (Gabo)	F_2	F_3	$BC_1(P_1)S_1$	$BC_1(P_1)S_1$
	(no. of pots)					
17 April 1986	-	-	45	30	30	30
19 April 1986	7	-	-	-	-	-
20 April 1986	36	-	-	-	-	-
21 April 1986	7	-	-	-	-	-
22 April 1986	-	-	90	70	60	60
23 April 1986	-	7	-	-	-	-
24 April 1986	-	23	-	-	-	-
25 April 1986	-	20	-	-	-	-
27 April 1986	-	-	45	30	30	30
Total	50	50	180	130	120	120

* Plants were transferred into climate rooms on June 16th, 1986.

Appendix 3.C. Planting dates and number of pots planted with the 6 generations of cross 3 wheat in PPD glasshouse before transferring to the controlled climate rooms*.

Date	Generations					
	P_1 (Tordo)	P_2 (Sonora)	F_2	F_3	$BC_1(P_1)S_1$	$BC_1(P_1)S_1$
	(no. of pots)					
2 March 1987	18	-	-	-	-	-
5 March 1987	-	-	43	43	22	22
9 March 1987	36	18	-	-	-	-
12 March 1987	-	-	86	86	44	44
16 March 1987	18	36	-	-	-	-
19 March 1987	-	-	43	43	22	22
23 March 1987	-	18	-	-	-	-
Total	72	72	172	172	88	88

* Plants were transferred into climate rooms on April 21st, 1987.

Appendix 4. Abbreviations and variable names used in the experiments.

Abbreviations	Names of variables
HR	Harvest ripeness
PI1	Amylase maturity (Phase Intersect 1)
PI2	GA-amylase maturity (Phase Intersect 2)
T50SG	Medin germination, time to median standard germination competency
T90SG	Germination maturity, time to 90% standard germination competency
T50PG	Median embryo maturity, or time to median potential germination
T90PG	Embryo maturity (Time to 90% potential germination)
T90DW	Dry weight maturity (Time to 90 % maximum grain dry weight)
T90COL	Grain colour maturity (Time to 90 % maximum colour score)
HRSG	Standard germination at harvest ripeness
HRPG	Potential germination at harvest ripeness
HRDW	Grain dry weight at harvest ripeness
MAXDW	Maximum grain dry weight
-	Base α-amylase at harvest ripeness
-	Base α-amylase at embryo maturity
-	Germinative α-amylase at harvest ripeness
-	Germinative α-amylase at embryo maturity
-	GA3 α-amylase at harvest ripeness
-	GA3 α-amylase at embryo maturity
MAXCOL	Maximum colour score
STRL	Percent sterility

Appendix 5. Expected mean squares in single environment analysis of variance, random effect model.

Source of variation	Degree of freedom	Mean square	Expected mean square	F ratio
Generations	g-1	M1	$\sigma^2 + b\,\sigma^2_G$	MS1/MS3
Blocks	b-1	M2	$\sigma^2 + g\,\sigma^2_B$	MS2/MS3
Error	(g-1)(b-1)	M3	σ^2	

g = number of generation; b = number of block.

Appendix 6. Expected mean squares in combined analysis of variance, random effect model.

Source of variation	Degree of freedom	Mean square	Expected mean square	F ratio
Environments	e-1	MS1	$\sigma^2 + g\,\sigma^2_B + b\,\sigma^2_{GE} + bg\,\sigma^2_E$	$\frac{(MS1 + MS5)}{(MS2 + MS4)}$
Blocks within environment	e(b-1)	MS2	$\sigma^2 + g\,\sigma^2_B$	MS2/MS5
Generations	g-1	MS3	$\sigma^2 + b\,\sigma^2_{GE} + be\,\sigma^2_G$	MS3/MS4
Generation x environment	(g-1)(e-1)	MS4	$\sigma^2 + b\,\sigma^2_{GE}$	MS4/MS5
Error	e(g-1)(b-1)	MS5	σ^2	

e = number of environment; g = number of generation; b = number of block within environment.

Appendix 7. Chi-square values in the test for homogeneity of error variances from the warm and the cool environments.

Variables	Cross 1	Cross 2	Cross 3
Harvest ripeness	14.009 [a] **	0.534 NS	0.440 NS
Amylase maturity	8.248 [a] **	2.397 NS	0.254 NS
GA-amylase maturity	0.114 NS	3.279 [a] (*)	2.096 NS
Median germination	-	-	0.625 NS
Germination maturity	-	-	2.359 NS
Median embryo maturity	0.000 NS	11.612 [a] **	2.697 [a] NS
Embryo maturity	0.079 (*)	5.164 [a] *	2.495 NS
Dry weight maturity	0.126 NS	14.600 [a] **	8.891 [a] **
Grain colour maturity	0.965 NS	0.273 NS	0.308 NS
Grain dry weight at harvest ripeness	0.466 NS	13.792 [a] **	0.262 NS
Maximum grain dry weight	0.924 NS	11.918 [a] **	0.469 NS
Base α-amylase at harvest ripeness	0.421 NS	2.447 NS	3.813 [a] (*)
Base α-amylase at embryo maturity	35.239 **	1.083 NS	0.46 NS
Germinative α-amylase at harvest ripeness	1.051 NS	0.013 NS	0.46 NS
Germinative α-amylase at embryo maturity	11.189 [a] **	4.541 [a] *	6.754 [a] **
GA_3 α-amylase at harvest ripeness	4.126 [a] *	0.170 NS	3.373 (*)
GA_3 α-amylase at embryo maturity	0.214 NS	9.625 [a] **	6.724 [a] **
Standard germination at harvest ripeness	-	2.247 NS	9.133 [a] **
Potential germination at harvest ripeness	0.069 NS	1.380 NS	4.314 [a] *
Maximum colour score	3.447 (*)	1.080 NS	0.000 NS
Sterility	0.078 NS	4.318 [a] *	1.384 NS

a : adjusted chi-square values.
NS : Chi-square not significant at the 10 % probability level.
(*): Chi-square significant at the 10 % probability level.
* : Chi-square significant at the 5% probability level.
** : Chi-square significant at the 1 % probability level.

APPENDICES

Figure A.1. Changes in moisture content during grain development of the six generations of cross 1 wheat ripening in the warm environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : $BC_1(Tordo)S_1$

F : $BC_1(Karamu)S_1$

* observed values in block 1.

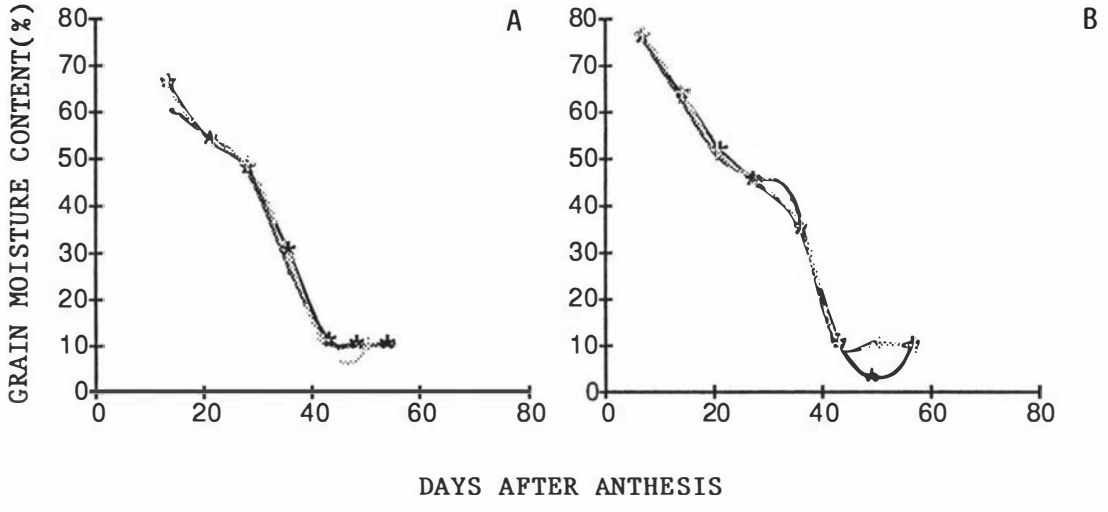
. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

——— predicted values in block 2.

···· ····· predicted values in block 3.


GRAIN MOISTURE CONTENT(%)
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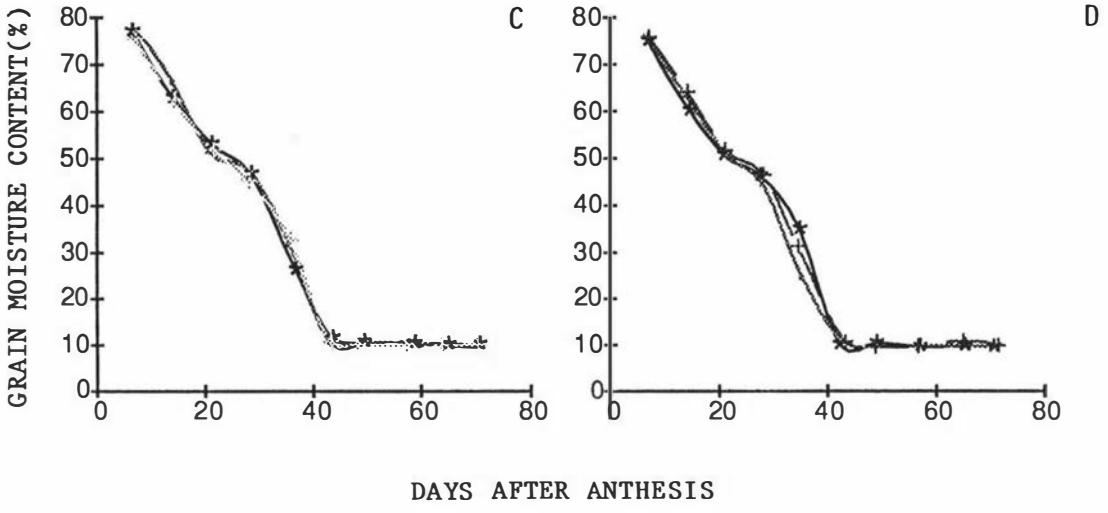
DAYS AFTER ANTHESIS


GRAIN MOISTURE CONTENT(%)
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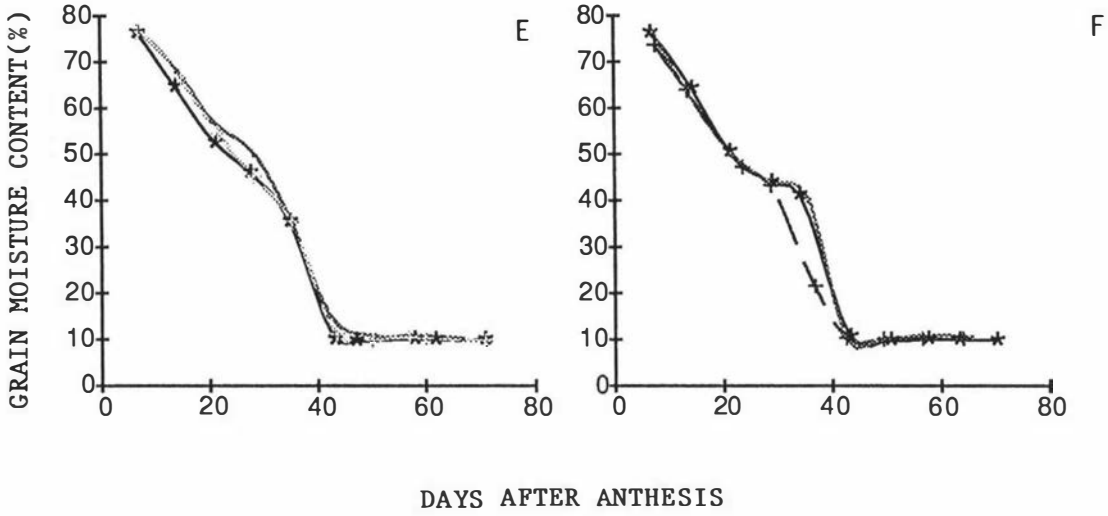
GRAIN MOISTURE CONTENT(%)
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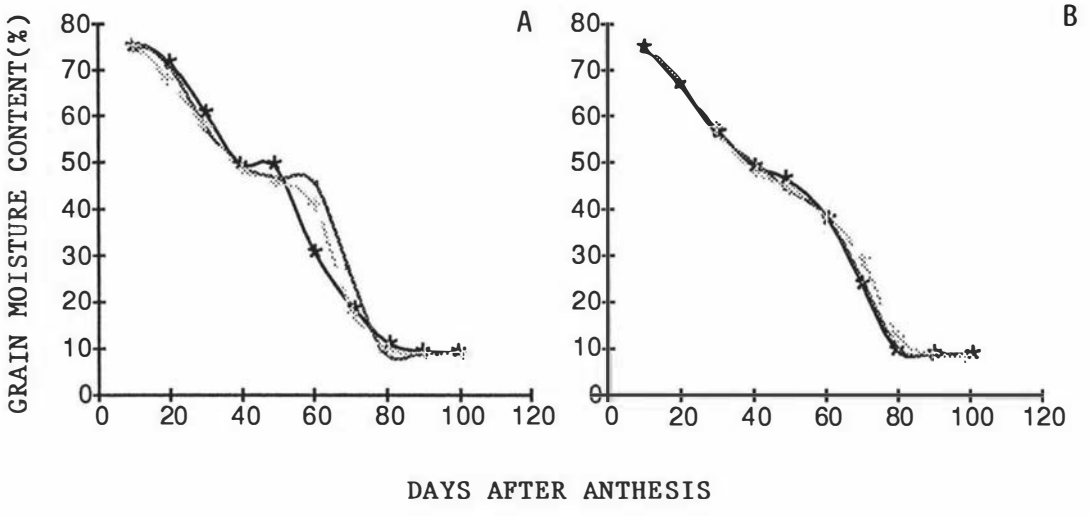
DAYS AFTER ANTHESIS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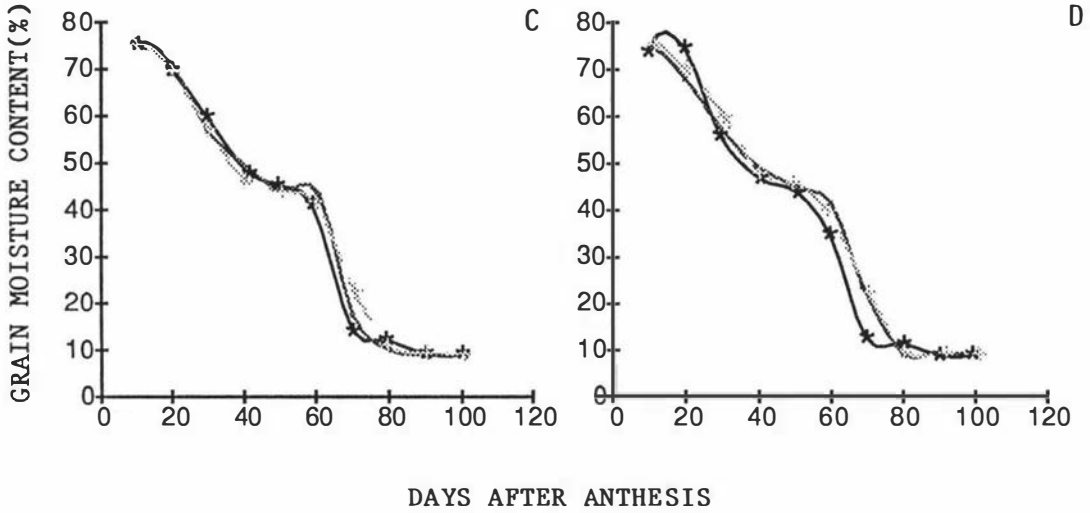
DAYS AFTER ANTHESIS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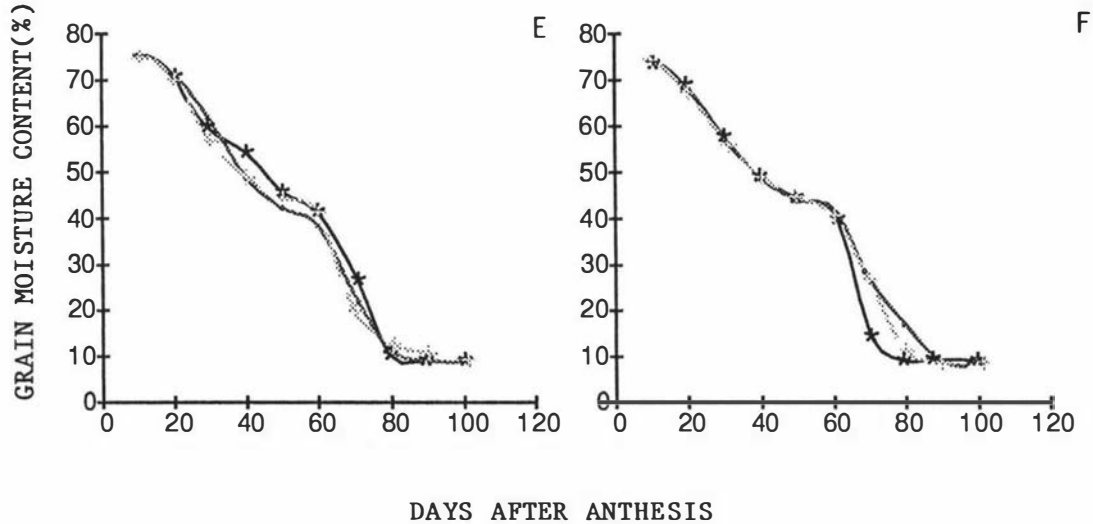
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GRAIN MOISTURE CONTENT(%)
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DAYS AFTER ANTHESIS

Figure A.3. Changes in moisture content during grain development of the six generations of cross 2 wheat ripening in the warm environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : $BC_1(Tordo)S_1$

F : $BC_1(Gabo)S_1$

* observed values in block 1.

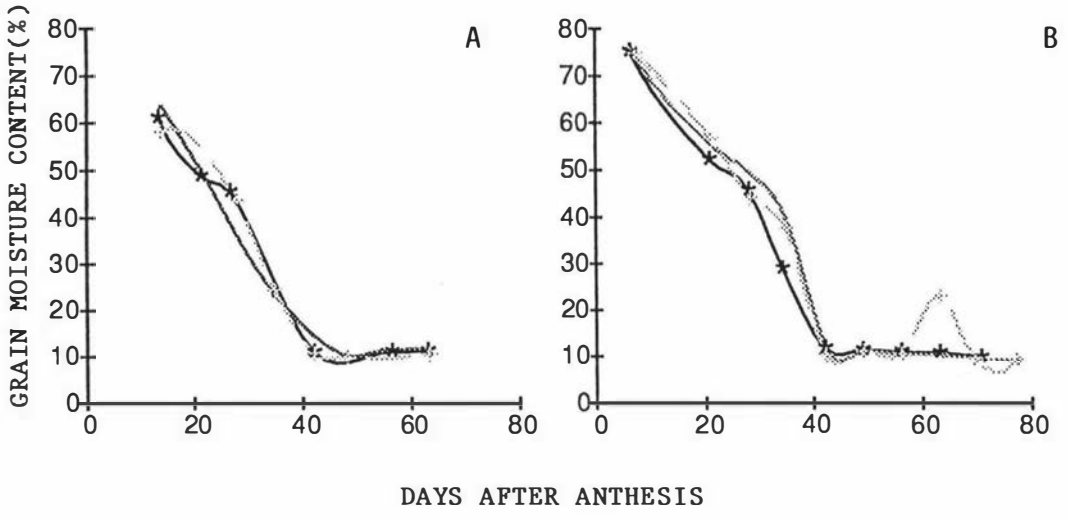
. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

——— predicted values in block 2.

···· ····· predicted values in block 3.


GRAIN MOISTURE CONTENT(%)
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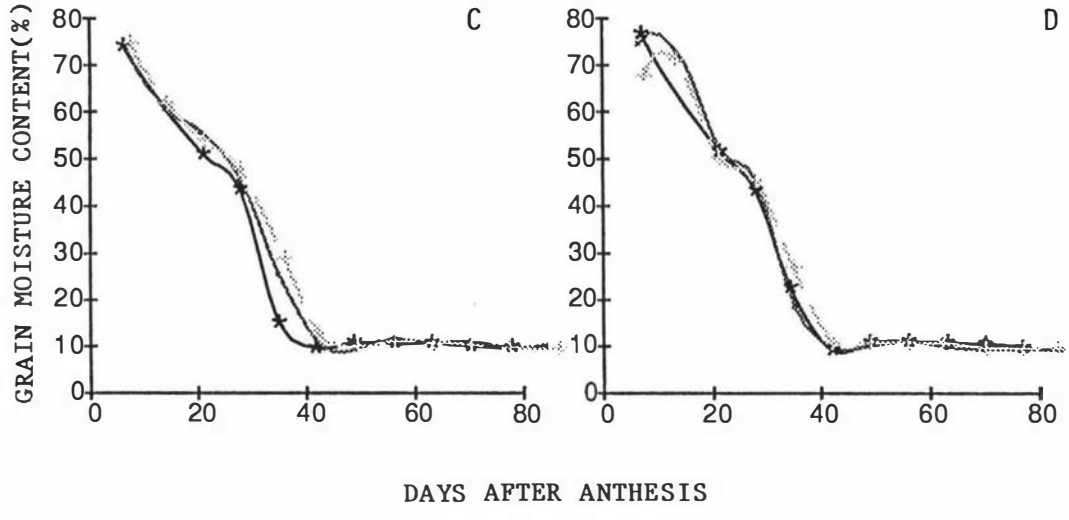
DAYS AFTER ANTHESIS


GRAIN MOISTURE CONTENT(%)
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80
DAYS AFTER ANTHESIS

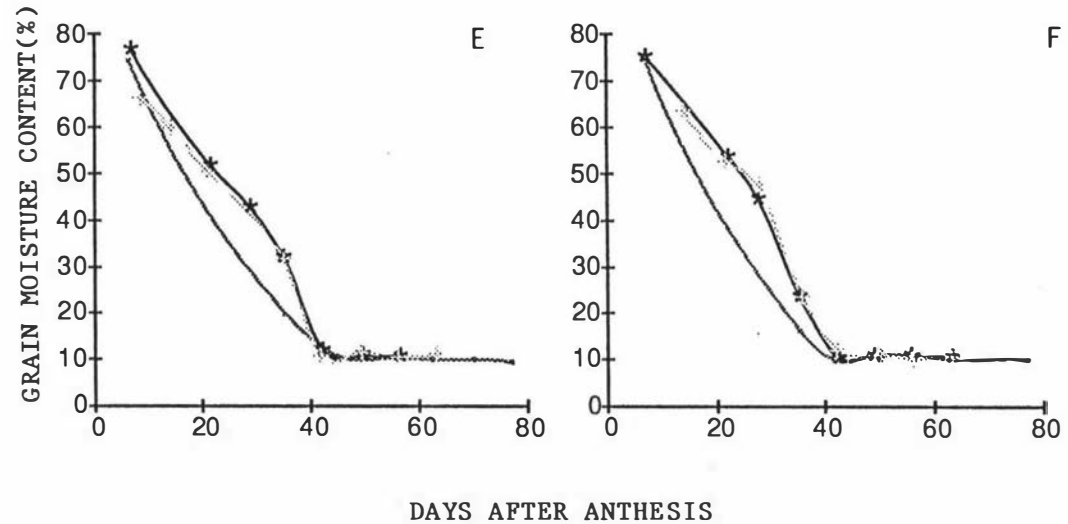

GRAIN MOISTURE CONTENT(%)
E
F
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.4. Changes in moisture content during grain development of the six generations of cross 2 wheat ripening in the cool environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : $BC_1(Tordo)S_1$

F : $BC_1(Gabo)S_1$

* observed values in block 1.

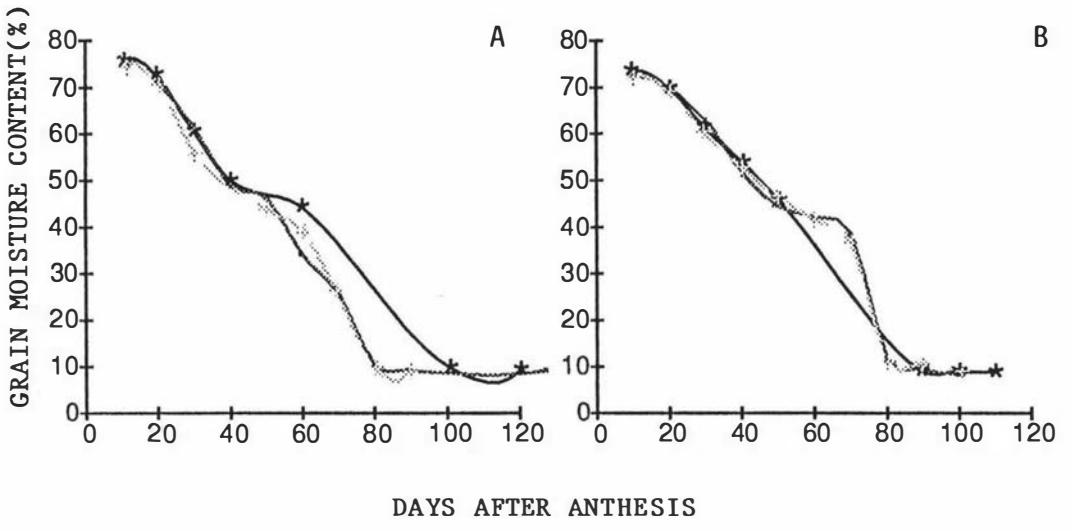
. observed values in block 2.

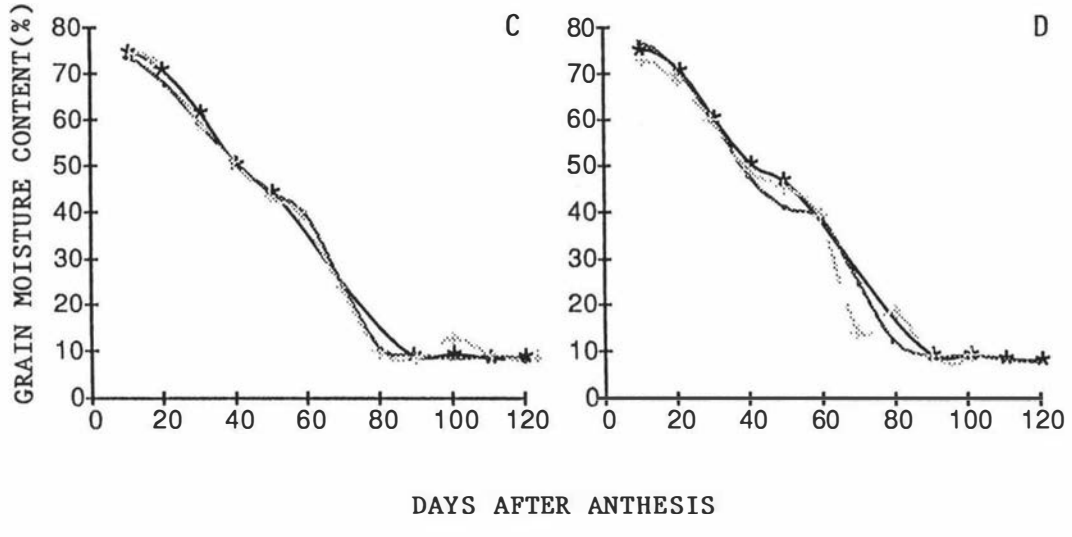
\+ observed values in block 3.

——— predicted values in block 1.

– – – – – predicted values in block 2.

···· ····· predicted values in block 3.


GRAIN MOISTURE CONTENT(%)
A
B
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS


GRAIN MOISTURE CONTENT(%)
C
D
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

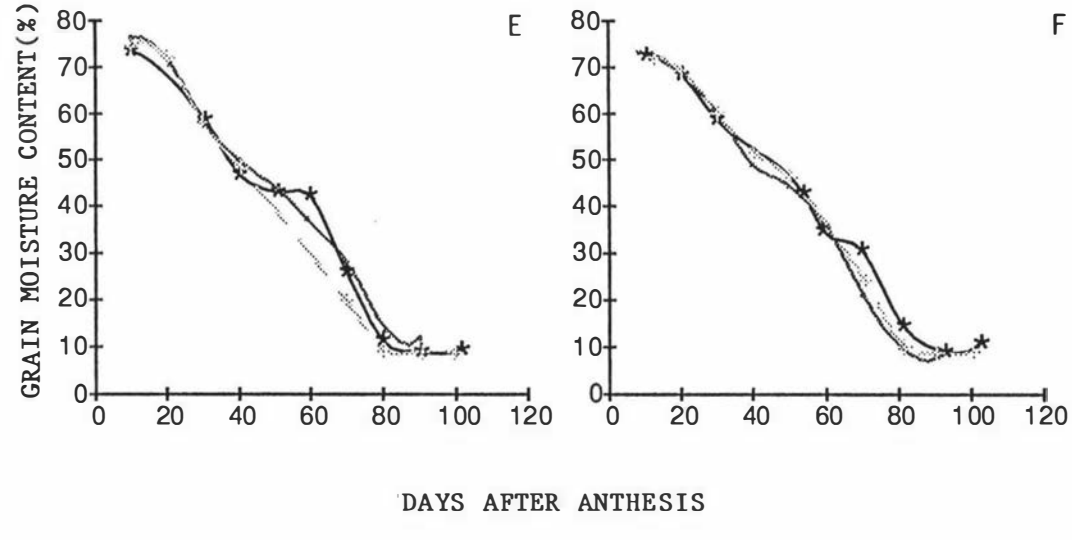

GRAIN MOISTURE CONTENT(%)
E
F
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.5. Changes in moisture content during grain development of the six generations of cross 3 wheat ripening in the warm environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

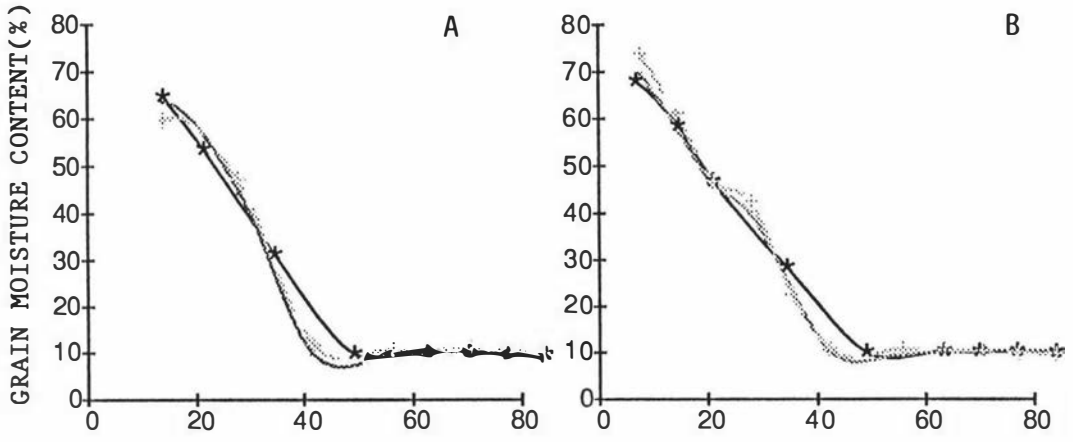
. observed values in block 2.

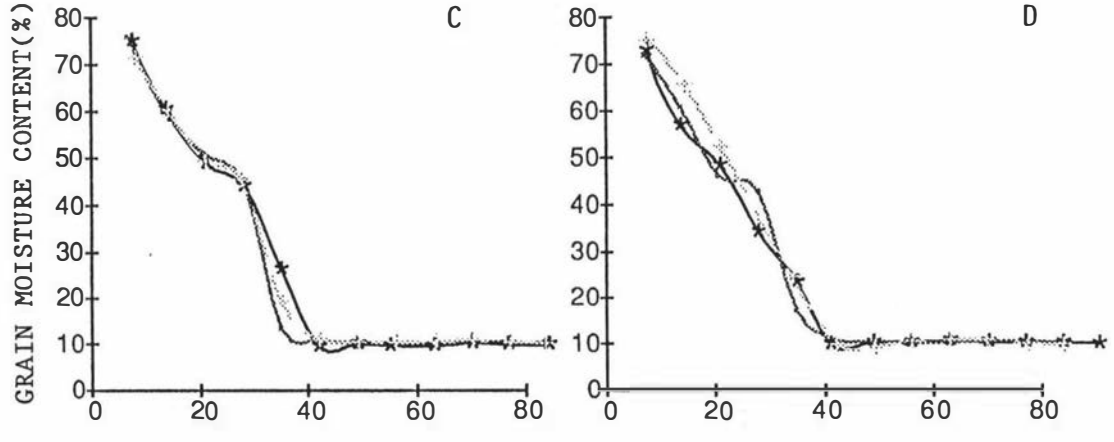
\+ observed values in block 3.

——— predicted values in block 1.

—— — predicted values in block 2.

···· ····· predicted values in block 3.


GRAIN MOISTURE CONTENT(%)
A
B
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS


GRAIN MOISTURE CONTENT(%)
C
D
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS

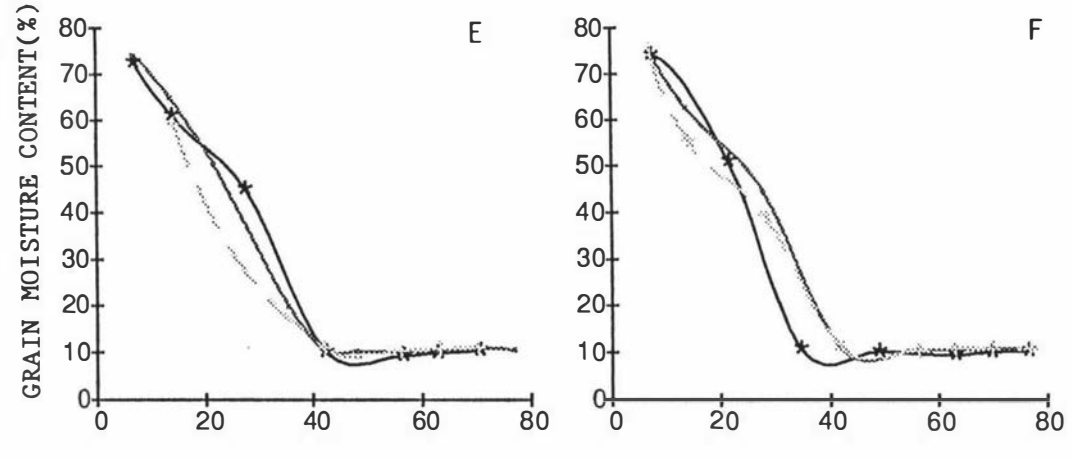

GRAIN MOISTURE CONTENT(%)
E
F
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.6. Changes in moisture content during grain development of the six generations of cross 3 wheat ripening in the cool environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

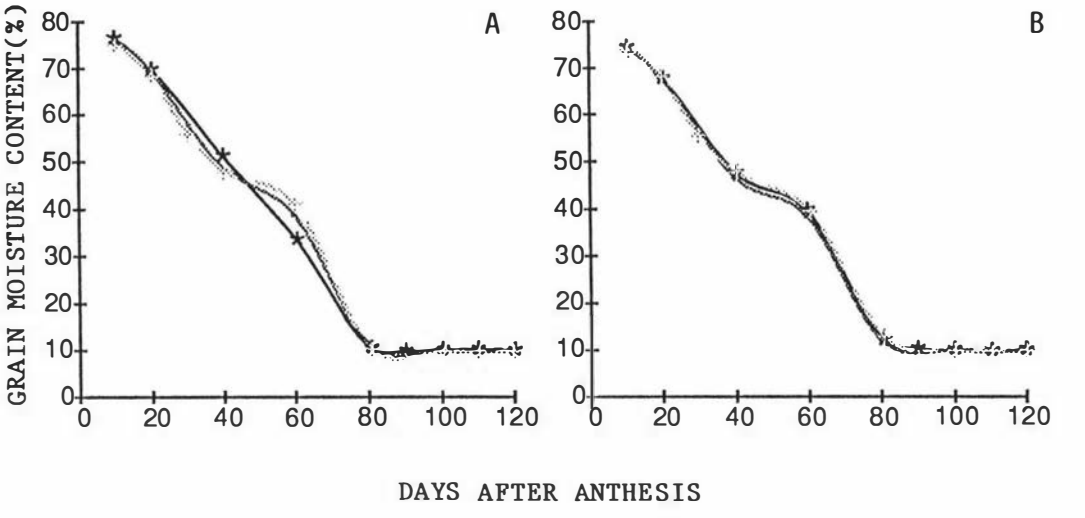
. observed values in block 2.

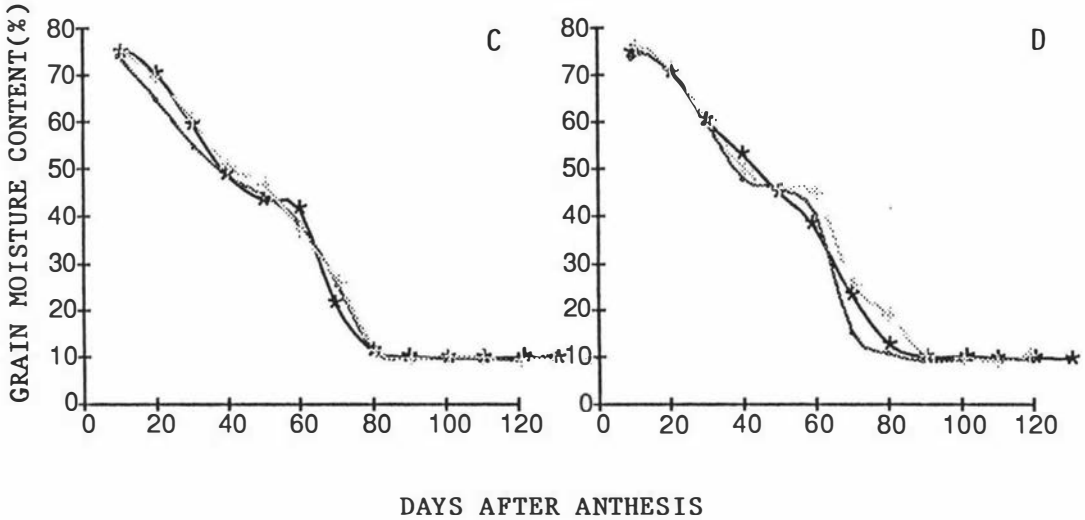
\+ observed values in block 3.

——— predicted values in block 1.

– – – – – predicted values in block 2.

···· ····· predicted values in block 3.


A
B
GRAIN MOISTURE CONTENT(%)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS


C
D
GRAIN MOISTURE CONTENT(%)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

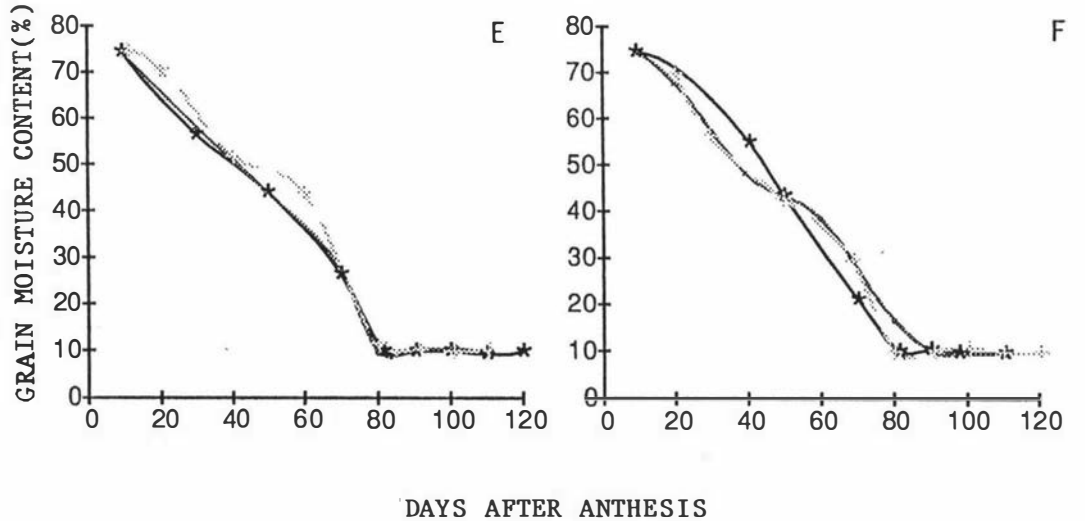

E
F
GRAIN MOISTURE CONTENT(%)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.7. Change in standard germination during grain development of the six generations of cross 1 wheat ripening in the warm environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

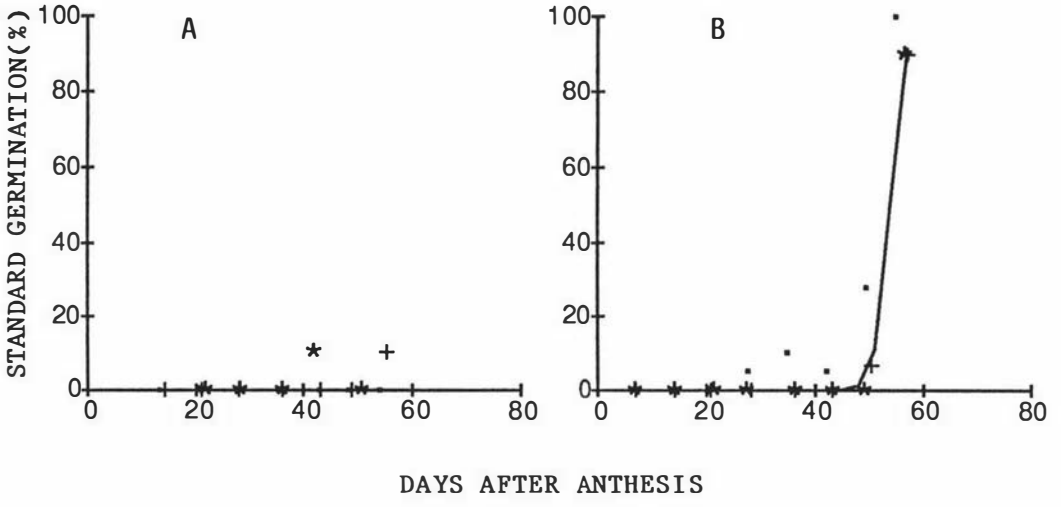
. observed values in block 2.

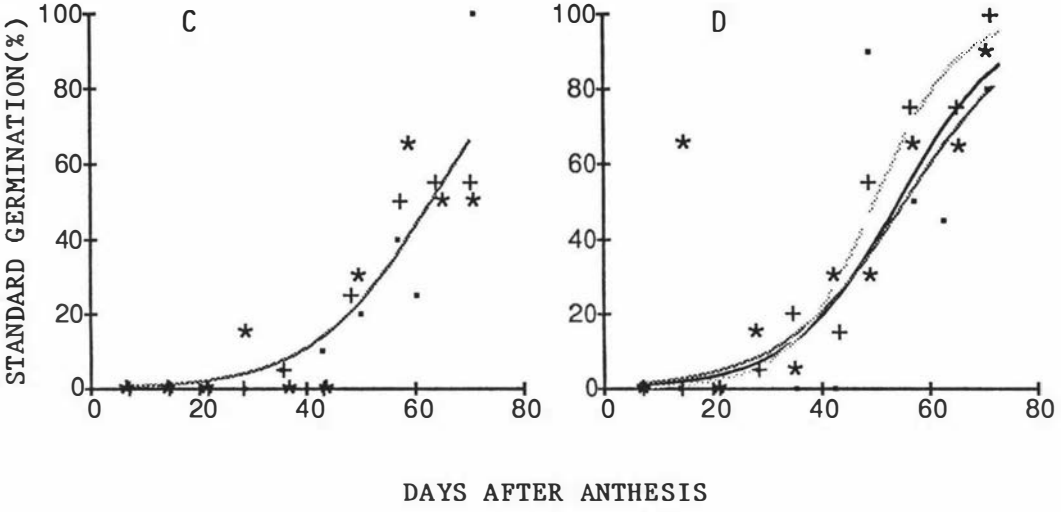
\+ observed values in block 3.

_____ predicted values in block 1.

_ _ _ _ _ predicted values in block 2.

.... predicted values in block 3.


A
B
STANDARD GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS


C
D
STANDARD GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS

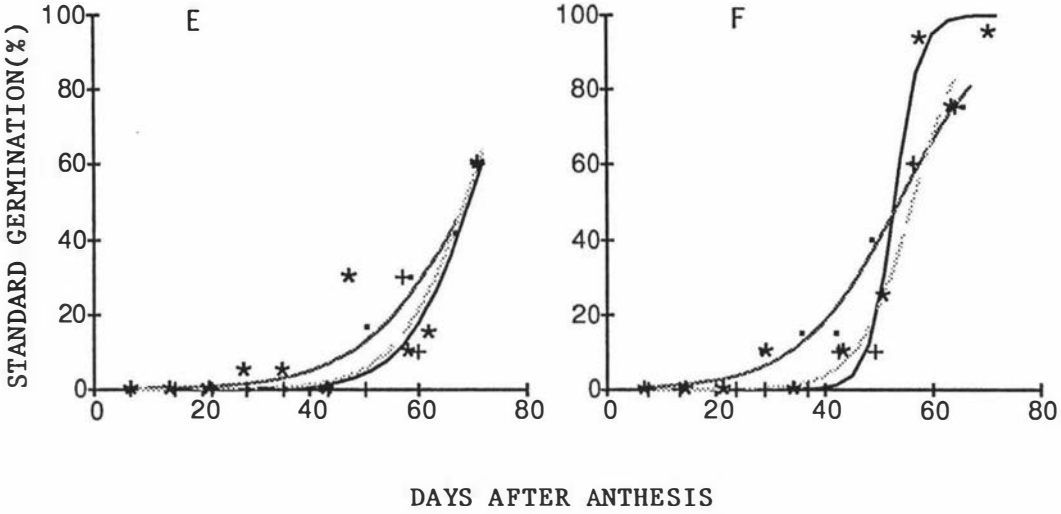

E
F
STANDARD GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.8. Change in standard germination during grain development of the six generations of cross 1 wheat ripening in the cool environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

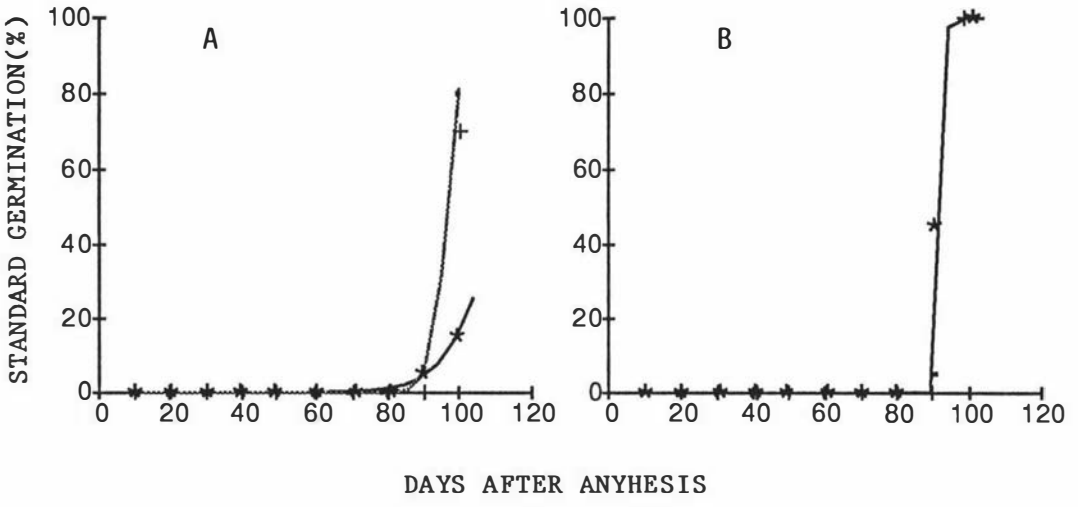
. observed values in block 2.

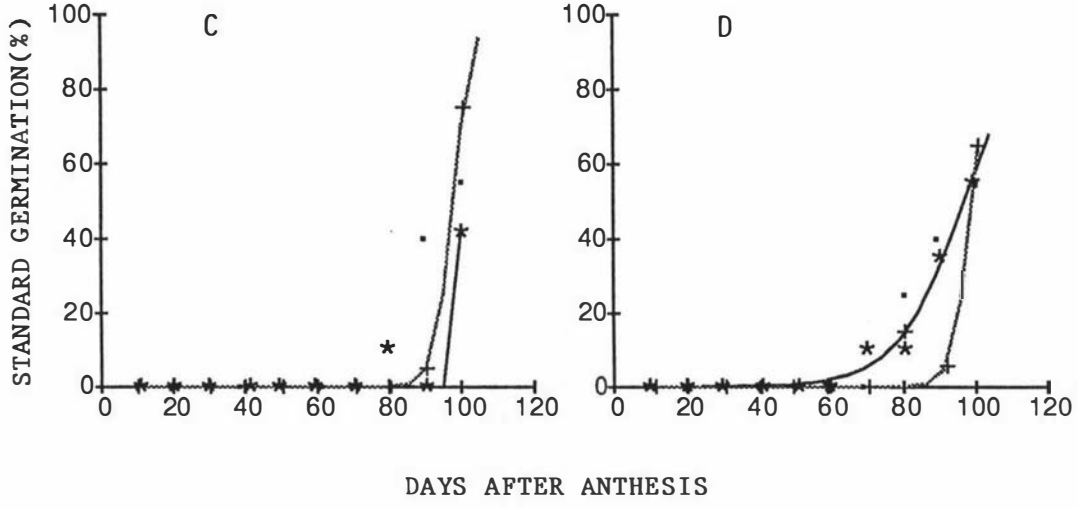
\+ observed values in block 3.

_____ predicted values in block 1.

_ _ _ _ _ predicted values in block 2.

.... predicted values in block 3.


A
B
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANYHESIS


C
D
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

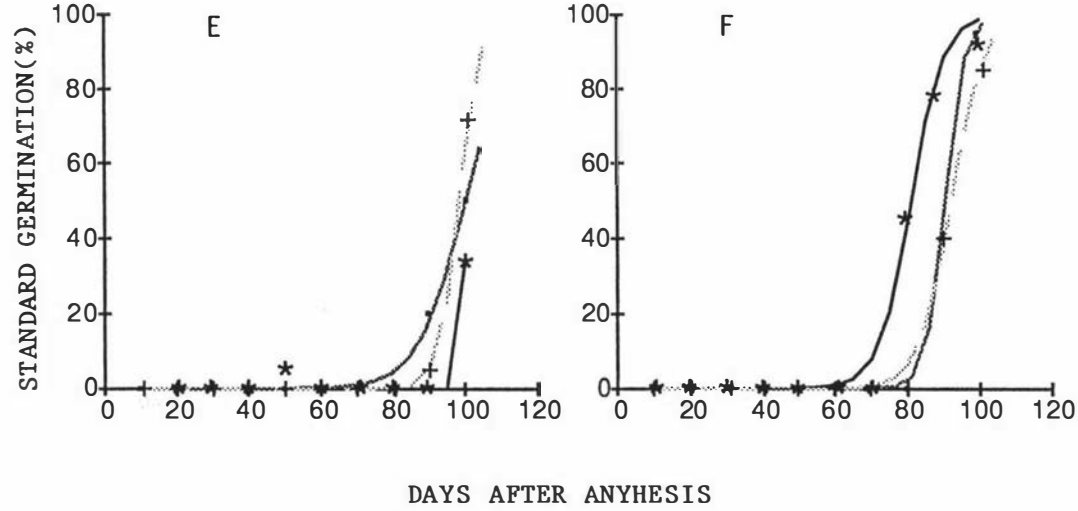

E
F
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANYHESIS

Figure A.9. Change in potential germination during grain development of the six generations of cross 1 wheat ripening in the warm environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

_____ predicted values in block 1.

_ _ _ _ _ predicted values in block 2.

.... predicted values in block 3.

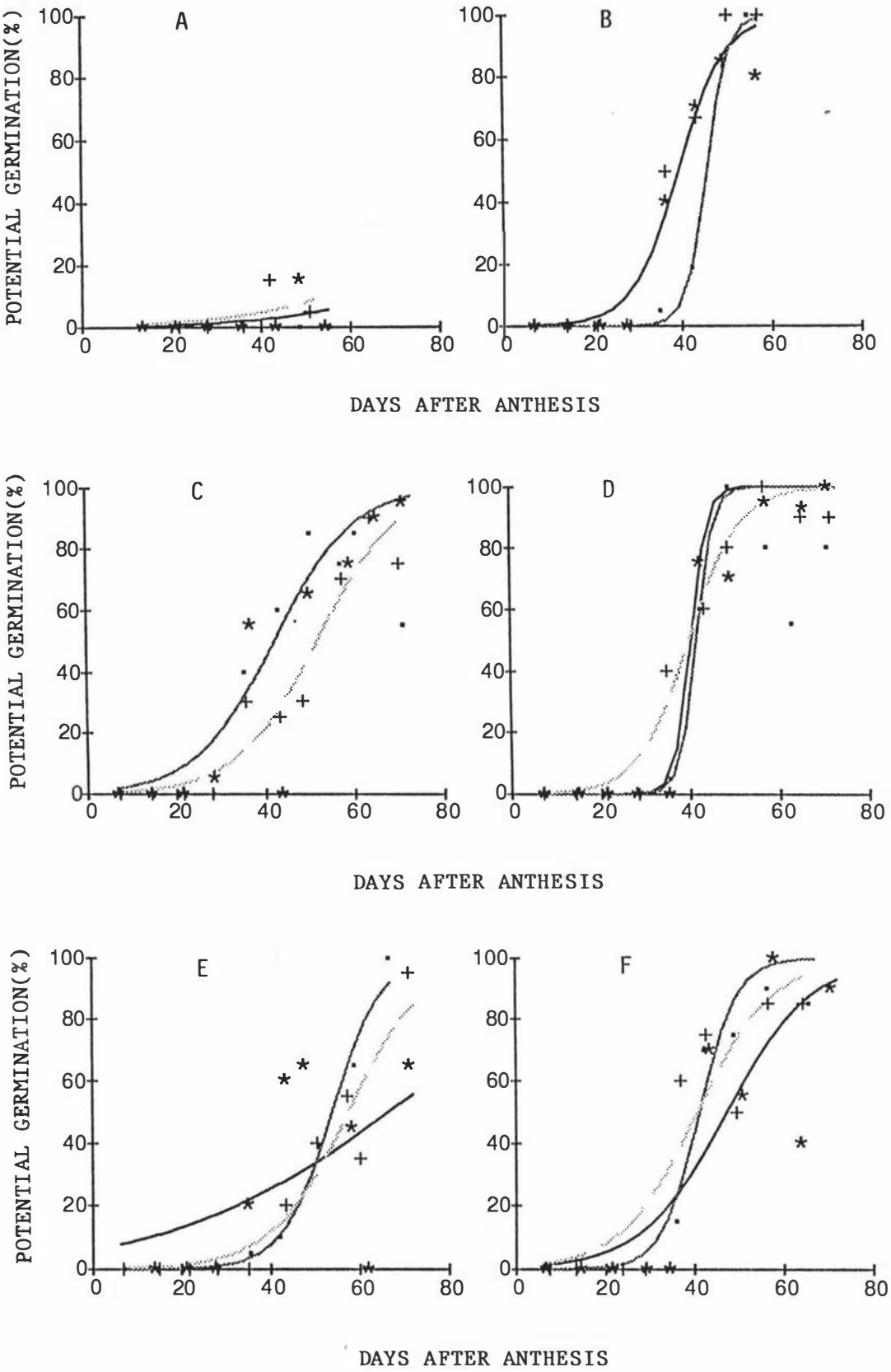

A
B
C
D
E
F
POTENTIAL GERMINATION(%)
DAYS AFTER ANTHESIS
0
20
40
60
80
100

Figure A.10. Change in potential germination during grain development of the six generations of cross 1 wheat ripening in the cool environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

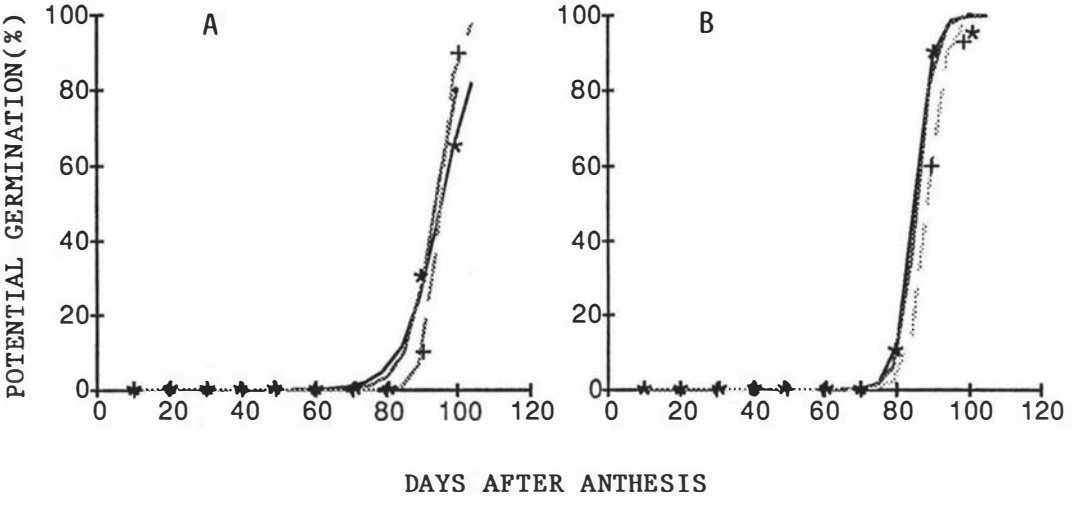
. observed values in block 2.

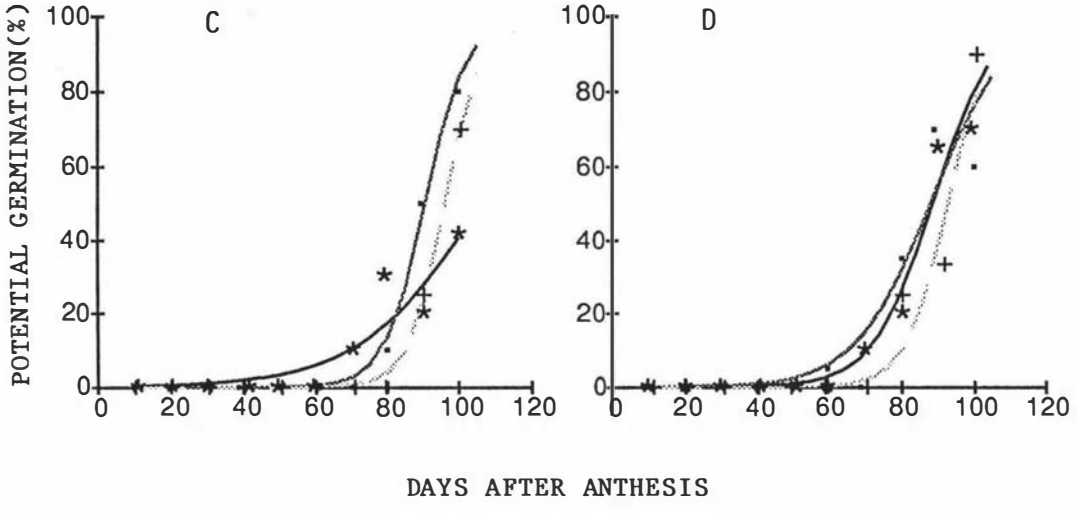
\+ observed values in block 3.

——— predicted values in block 1.

– – – – predicted values in block 2.

.... predicted values in block 3.


A
B
POTENTIAL GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS


C
D
POTENTIAL GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

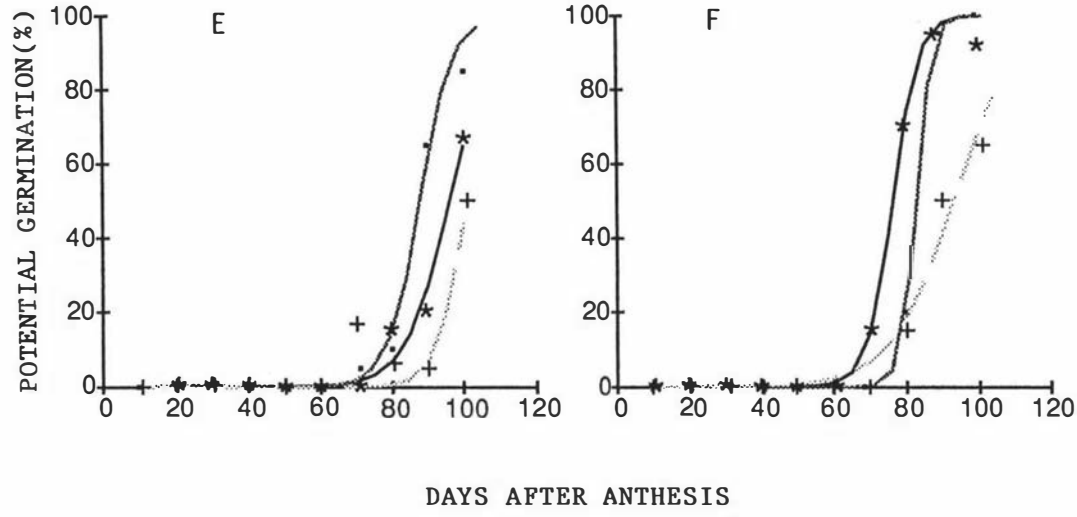

E
F
POTENTIAL GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

Figure A.11. Change in standard germination during grain development of the six generations of cross 2 wheat ripening in the warm environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

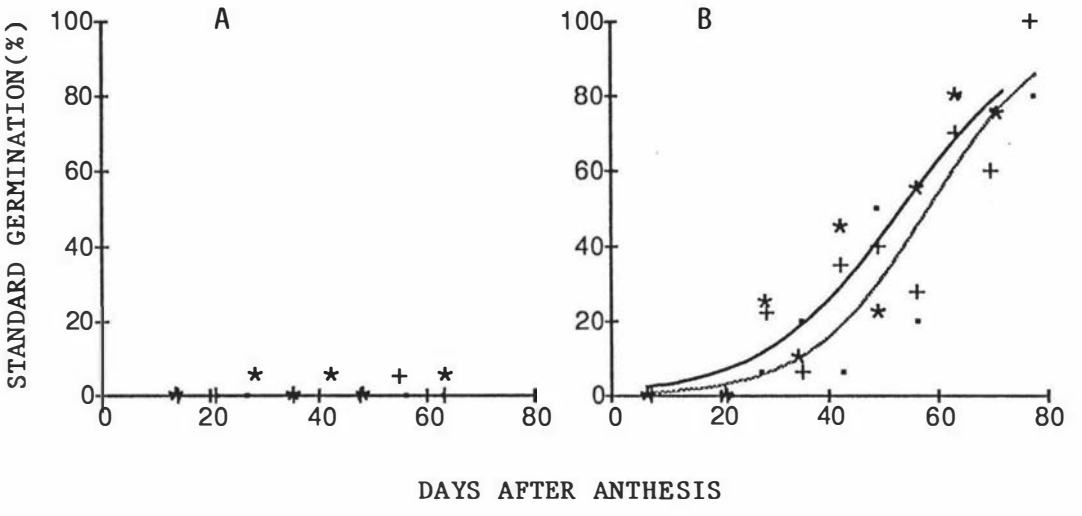
. observed values in block 2.

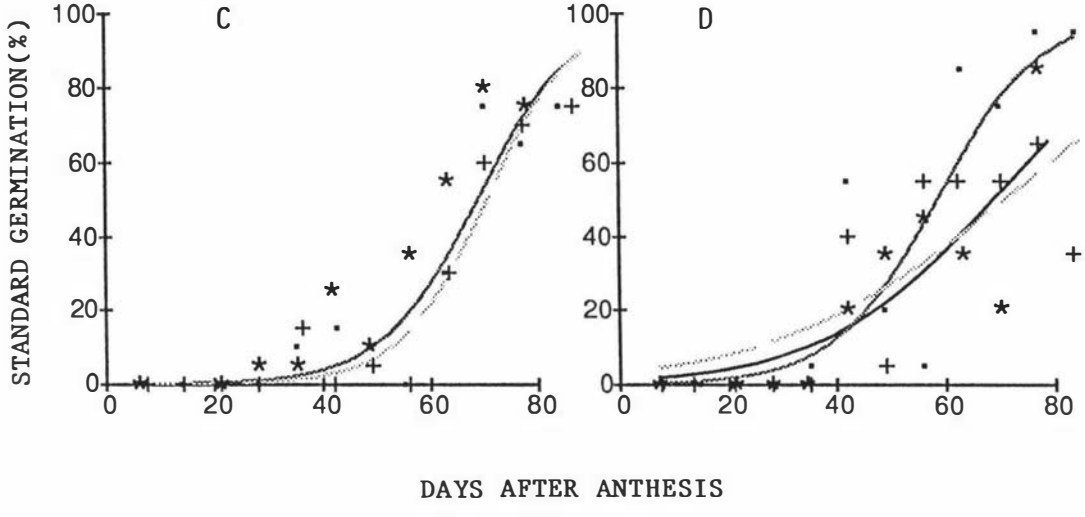
\+ observed values in block 3.

——— predicted values in block 1.

-——— predicted values in block 2.

.... predicted values in block 3.


A
B
STANDARD GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS


C
D
STANDARD GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS

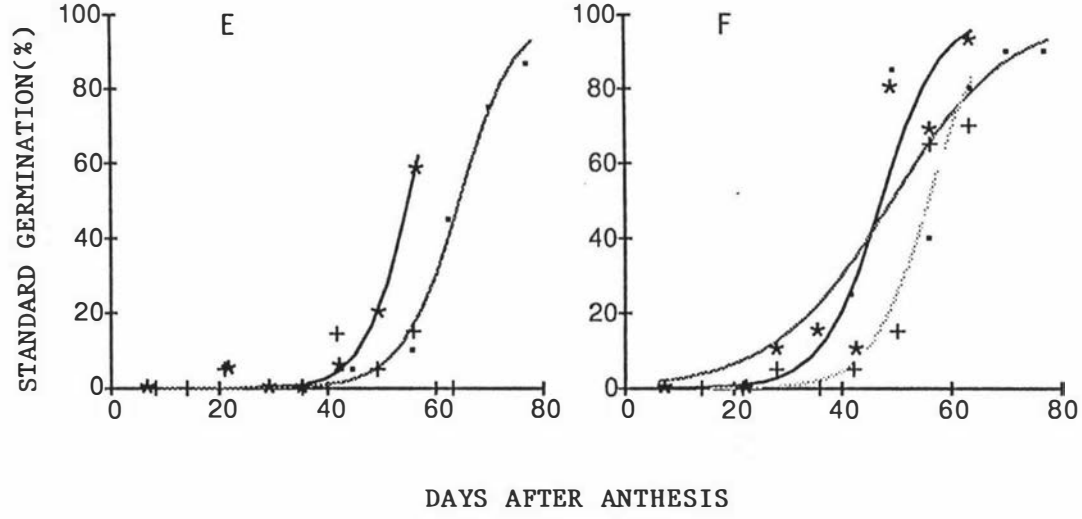

E
F
STANDARD GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.12. Change in standard germination during grain development of the six generations of cross 2 wheat ripening in the cool environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

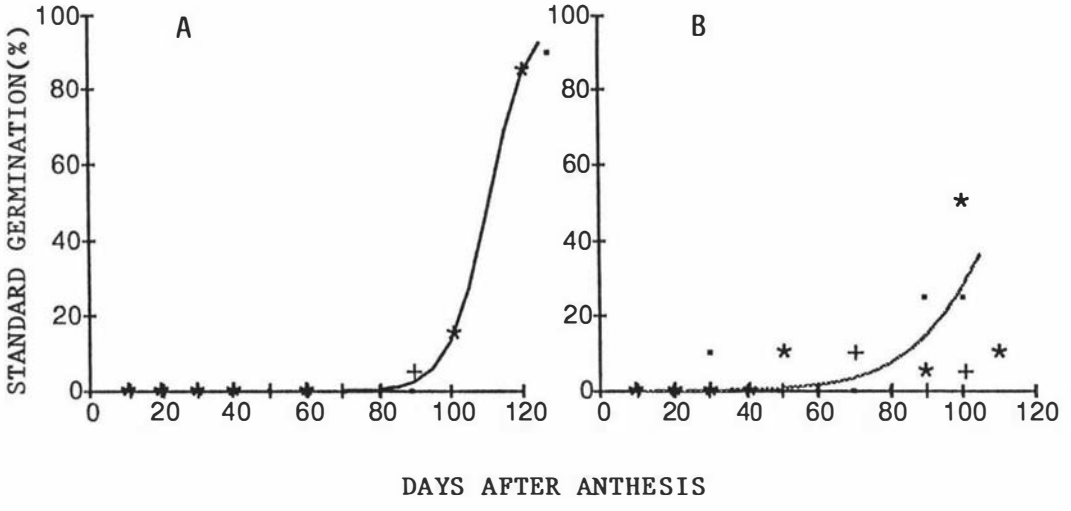
. observed values in block 2.

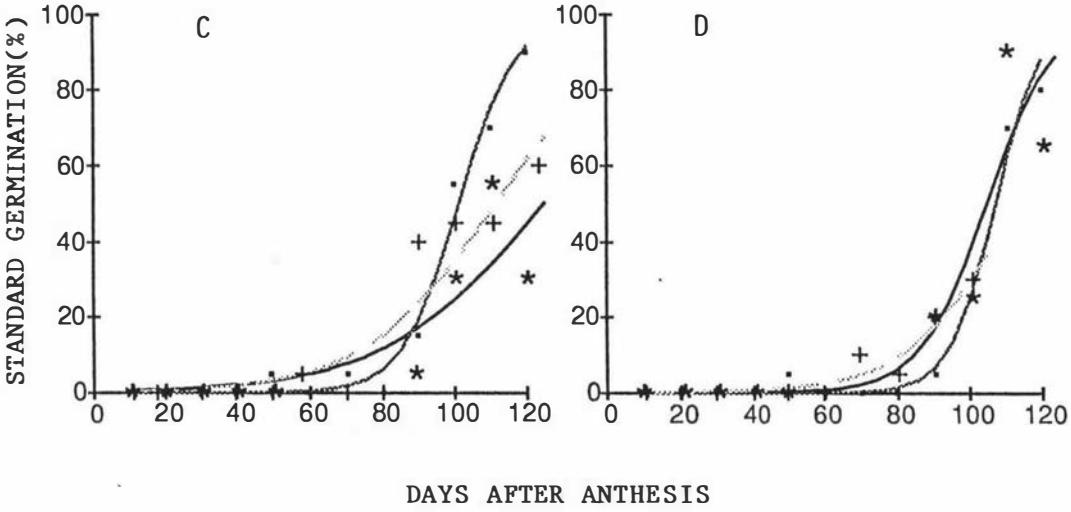
\+ observed values in block 3.

——— predicted values in block 1.

– – – – – – predicted values in block 2.

.... predicted values in block 3.


A
B
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS


C
D
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

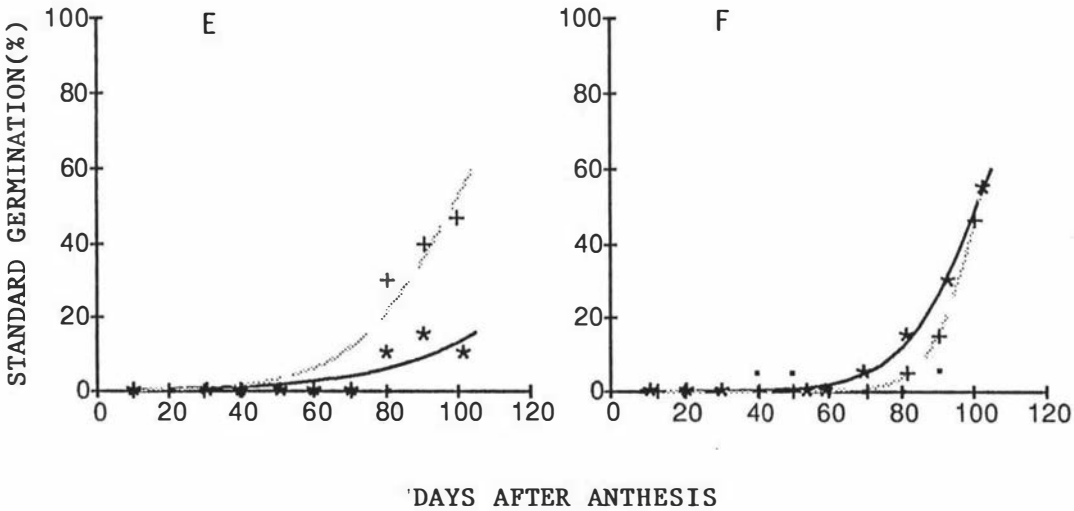

E
F
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

Figure A.13. Change in potential germination during grain development of the six generations of cross 2 wheat ripening in the warm environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : $BC_1(Tordo)S_1$

F : $BC_1(Gabo)S_1$

* observed values in block 1.

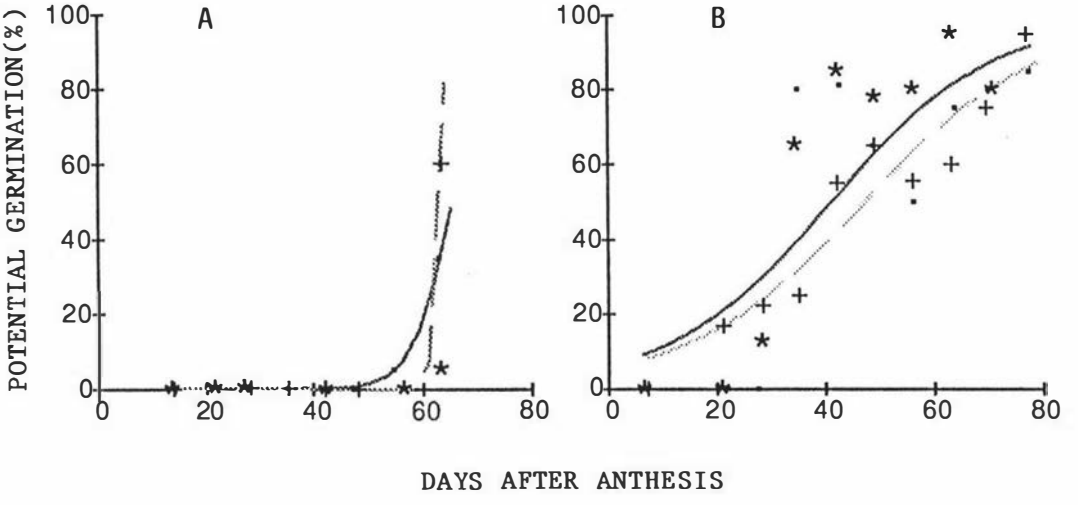
. observed values in block 2.

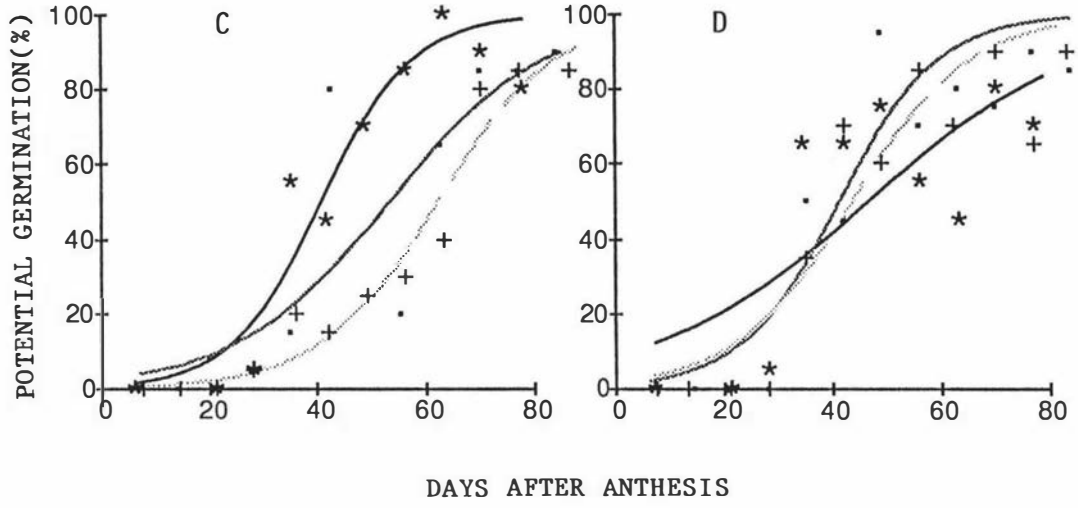
\+ observed values in block 3.

_____ predicted values in block 1.

_____ predicted values in block 2.

.... predicted values in block 3.


A
B
POTENTIAL GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS


C
D
POTENTIAL GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS

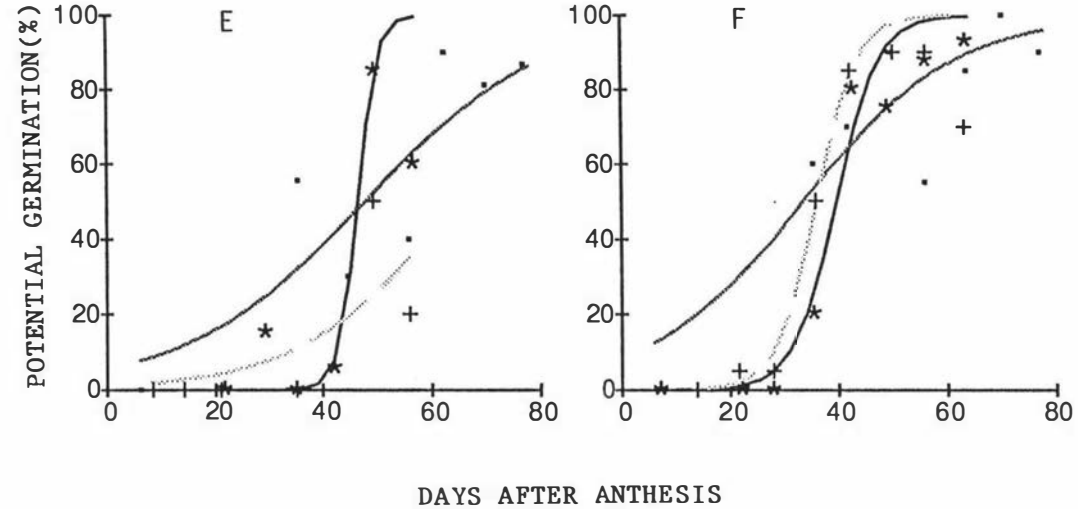

E
F
POTENTIAL GERMINATION(%)
100
80
60
40
20
0
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.14. Change in potential germination during grain development of the six generations of cross 2 wheat ripening in the cool environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

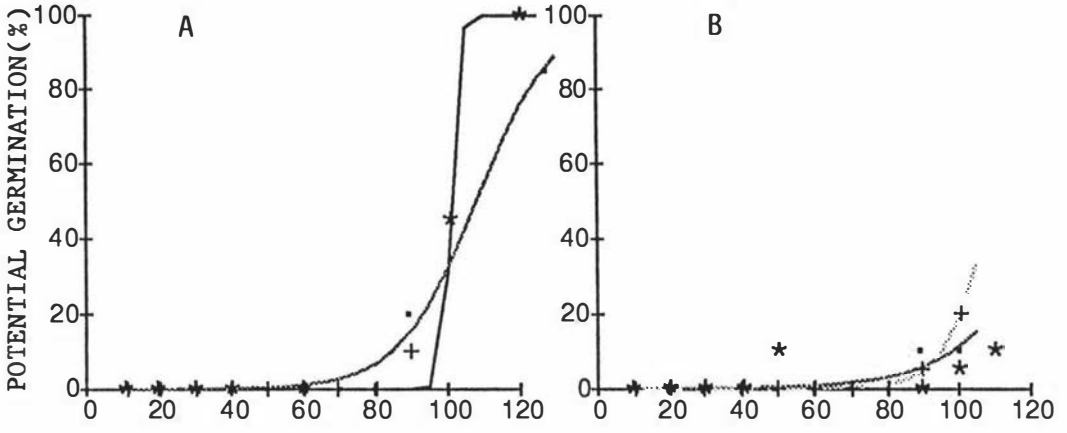
. observed values in block 2.

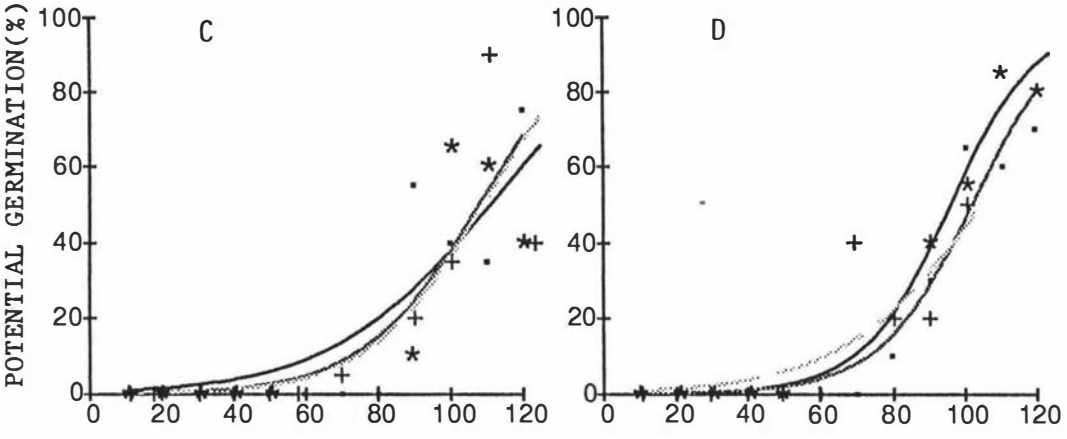
\+ observed values in block 3.

——— predicted values in block 1.

_——— predicted values in block 2.

.... predicted values in block 3.


A
B
POTENTIAL GERMINATION(%)
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS


C
D
POTENTIAL GERMINATION(%)
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

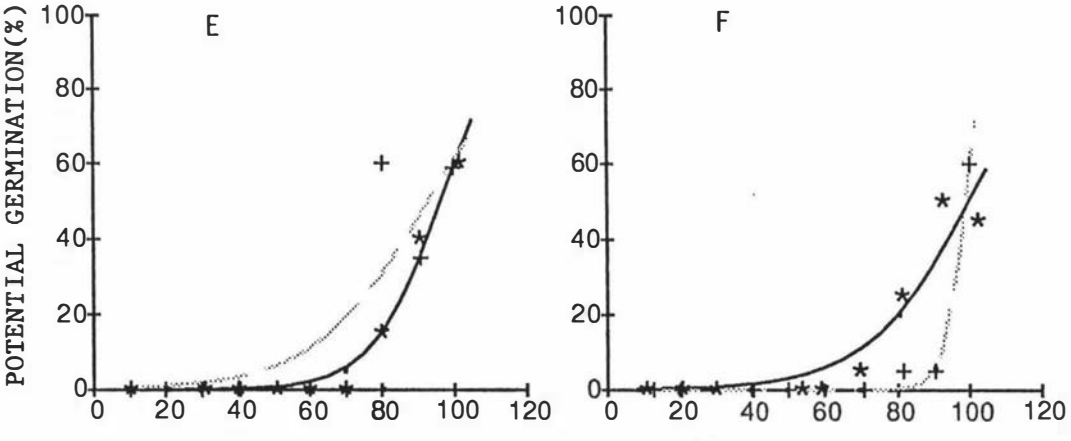

E
F
POTENTIAL GERMINATION(%)
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.15. Change in standard germination during grain development of the six generations of cross 3 wheat ripening in the warm environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

- - - - - - - - predicted values in block 2.

.... predicted values in block 3.

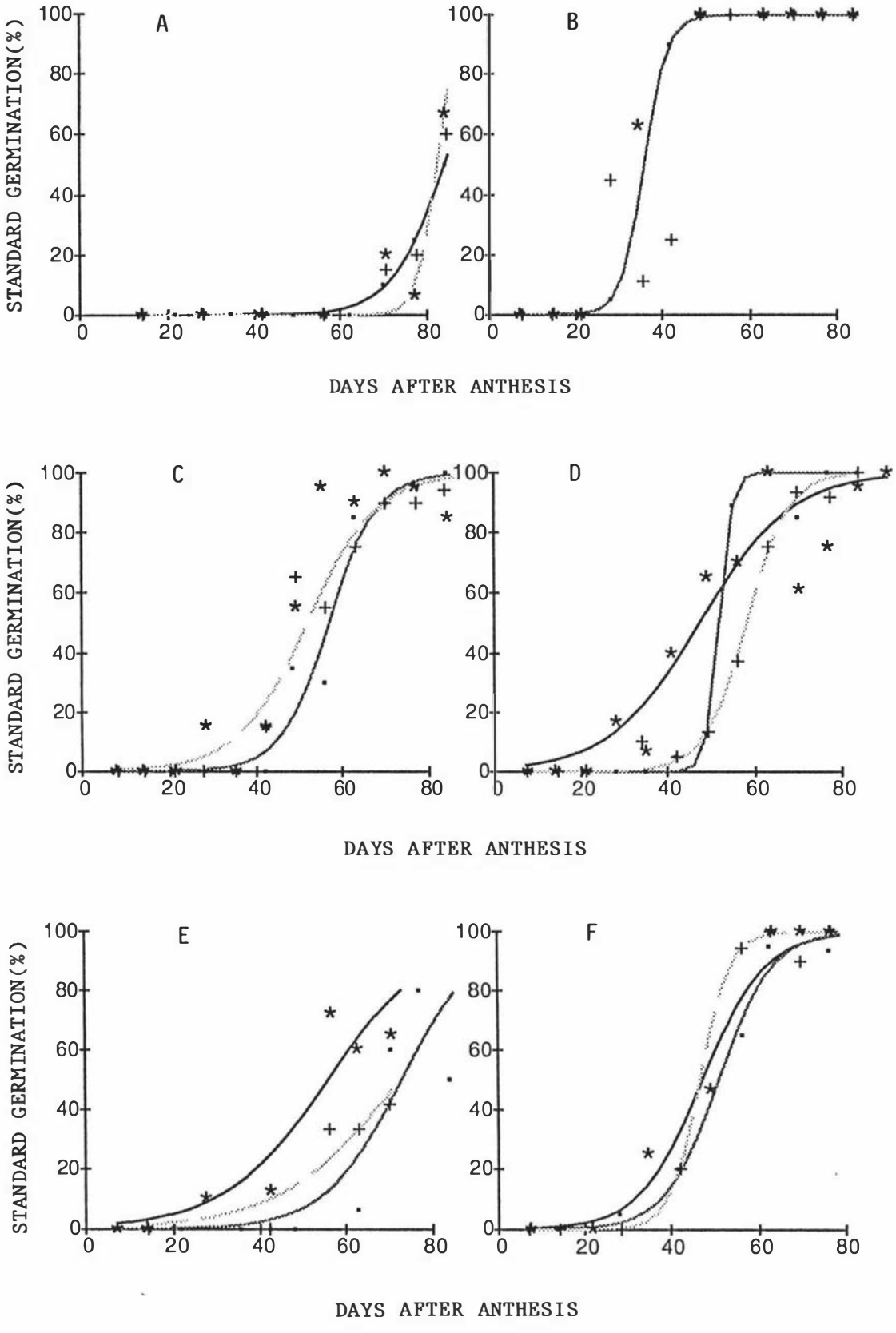

A
B
C
D
E
F
STANDARD GERMINATION(%)
DAYS AFTER ANTHESIS
0
20
40
60
80
100

Figure A.16. Change in standard germination during grain development of the six generations of cross 3 wheat ripening in the cool environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

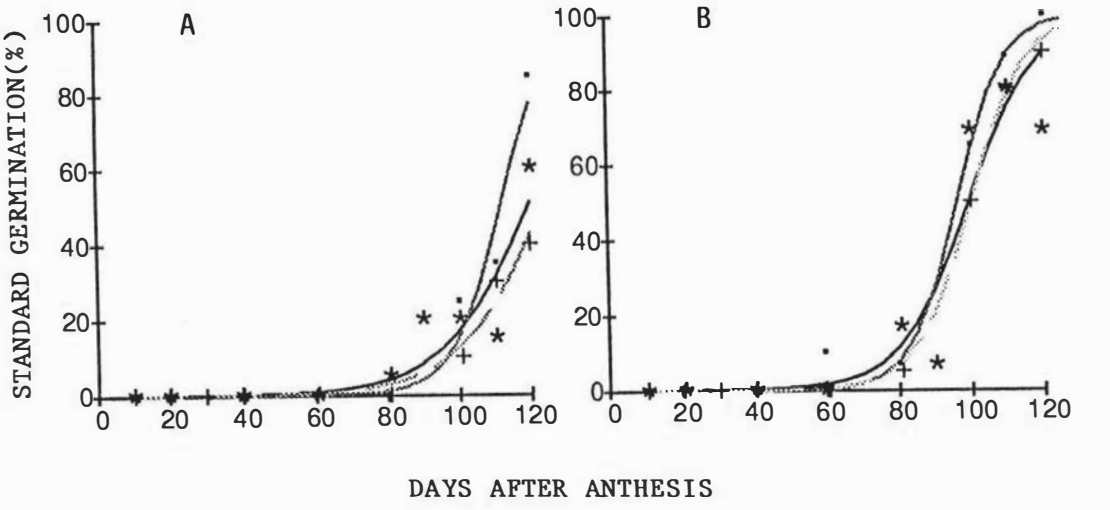
. observed values in block 2.

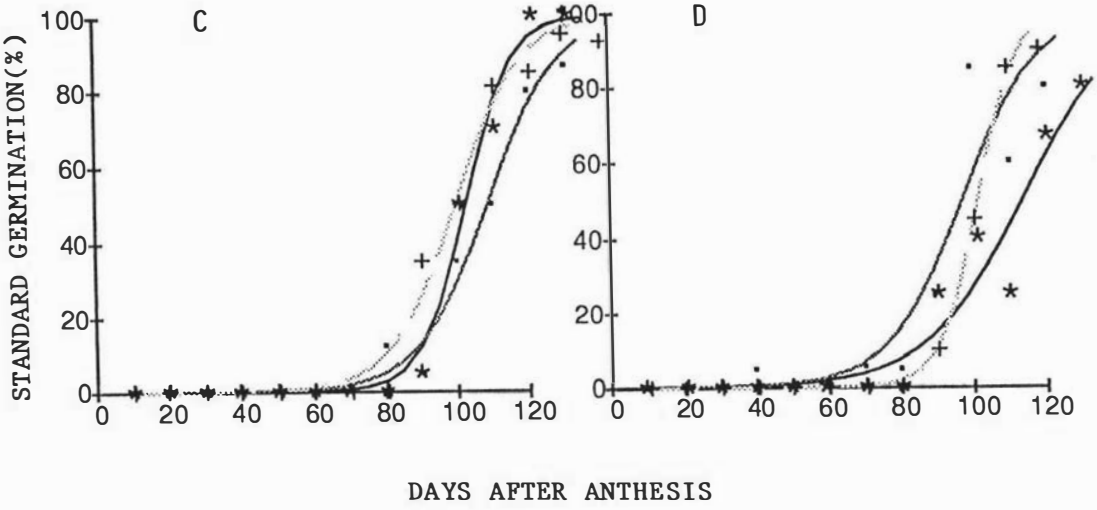
\+ observed values in block 3.

——— predicted values in block 1.

_ _ _ _ predicted values in block 2.

.... predicted values in block 3.


A
B
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS


C
D
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

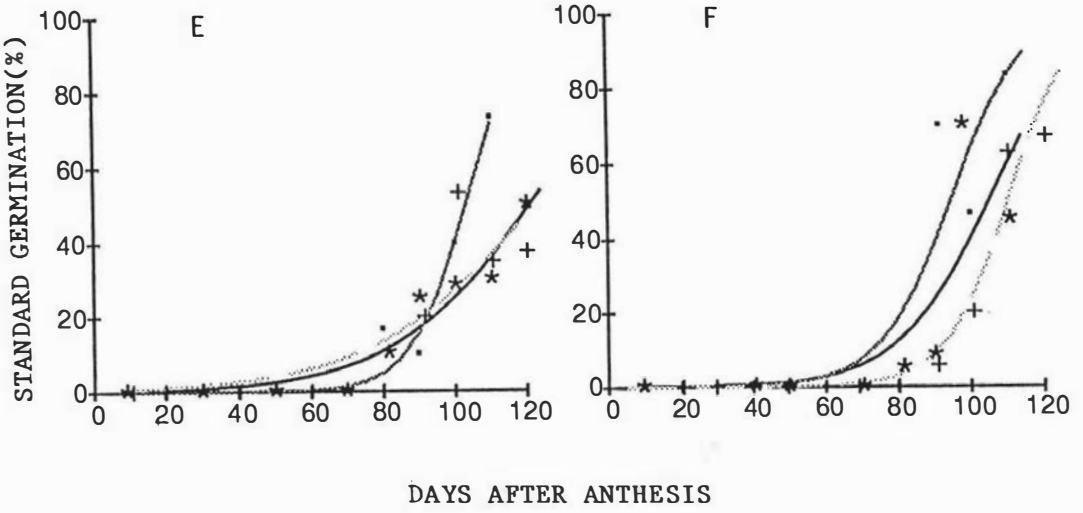

E
F
STANDARD GERMINATION(%)
100
80
60
40
20
0
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

Figure A.17. Change in potential germination during grain development of the six generations of cross 3 wheat ripening in the warm environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

– – – – – – predicted values in block 2.

···· ····· predicted values in block 3.

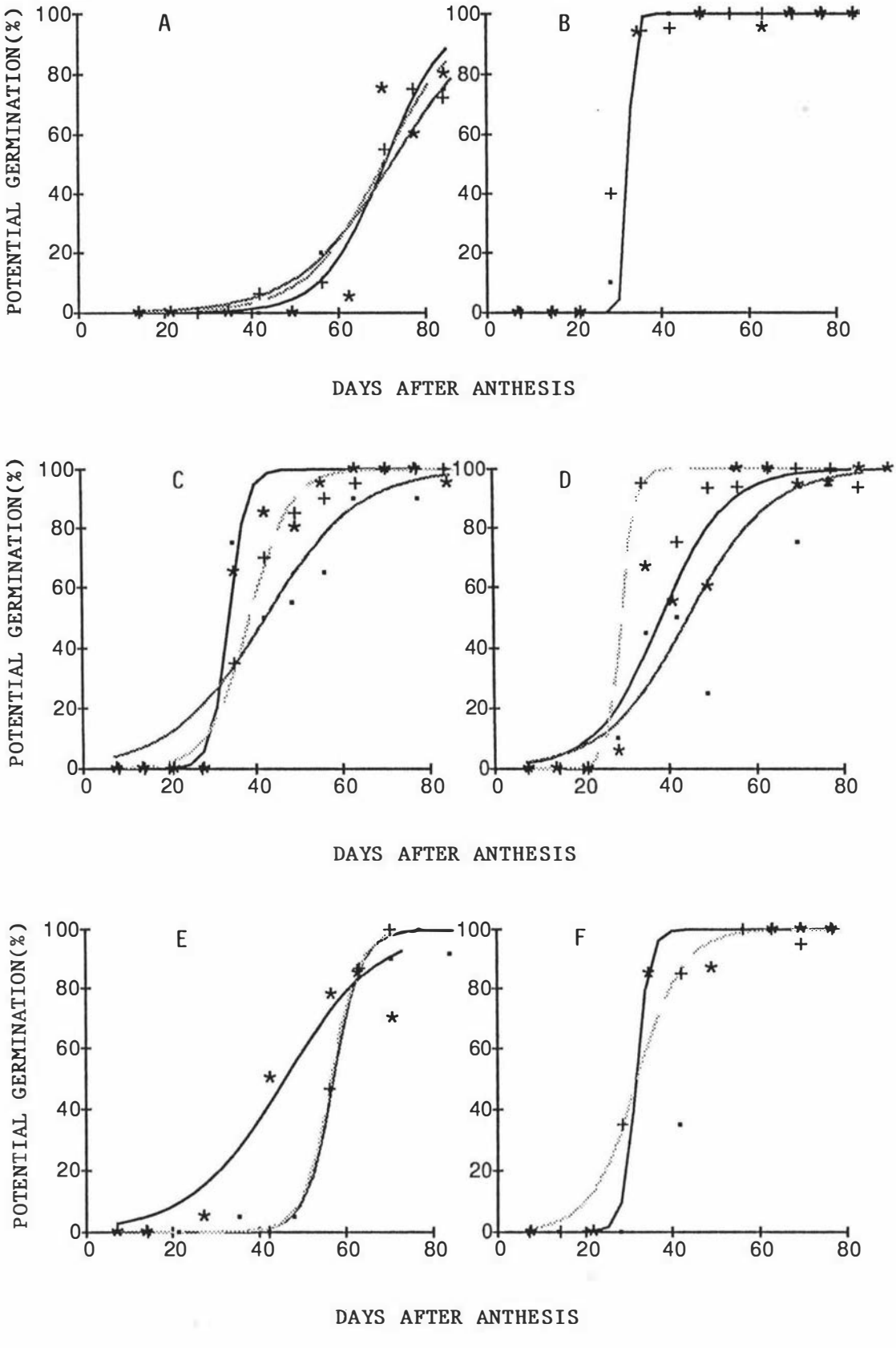

A
B
C
D
E
F
POTENTIAL GERMINATION(%)
DAYS AFTER ANTHESIS
0
20
40
60
80
100

Figure A.18. Change in potential germination during grain development of the six generations of cross 3 wheat ripening in the cool environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

– – – – – predicted values in block 2.

···· ····· predicted values in block 3.

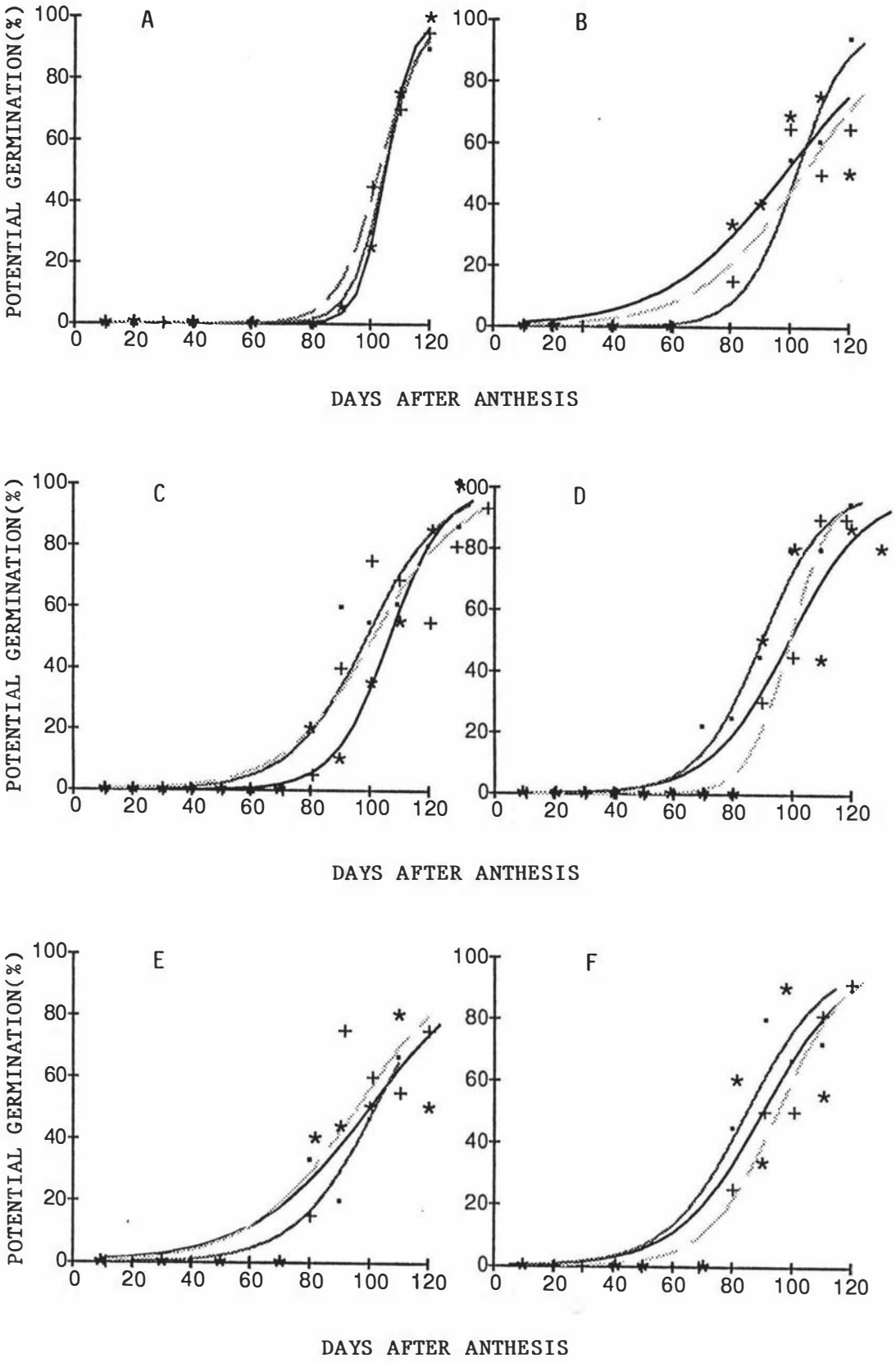

A
B
C
D
E
F
POTENTIAL GERMINATION(%)
DAYS AFTER ANTHESIS
0
20
40
60
80
100
120

Figure A.19. Change in grain dry weight during grain development of the six generations of cross 1 wheat ripening in the warm environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

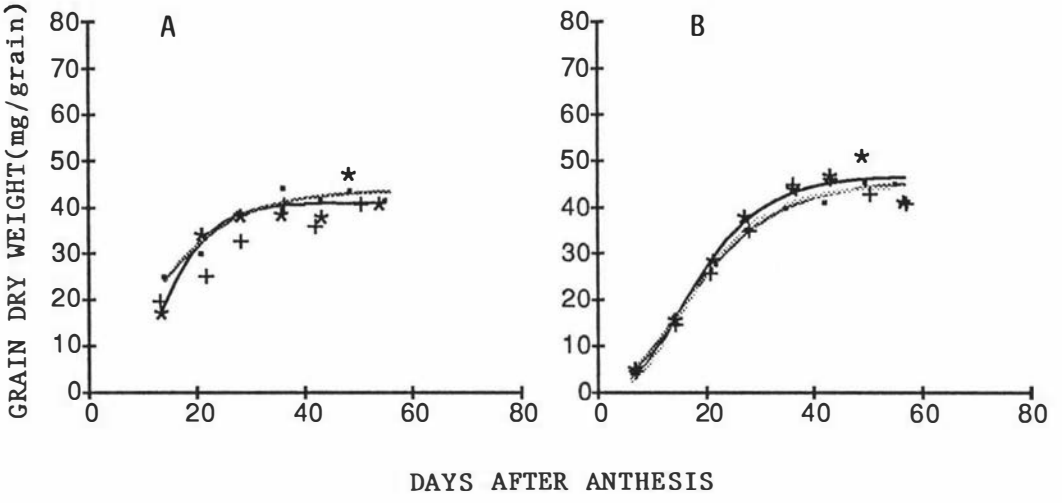
. observed values in block 2.

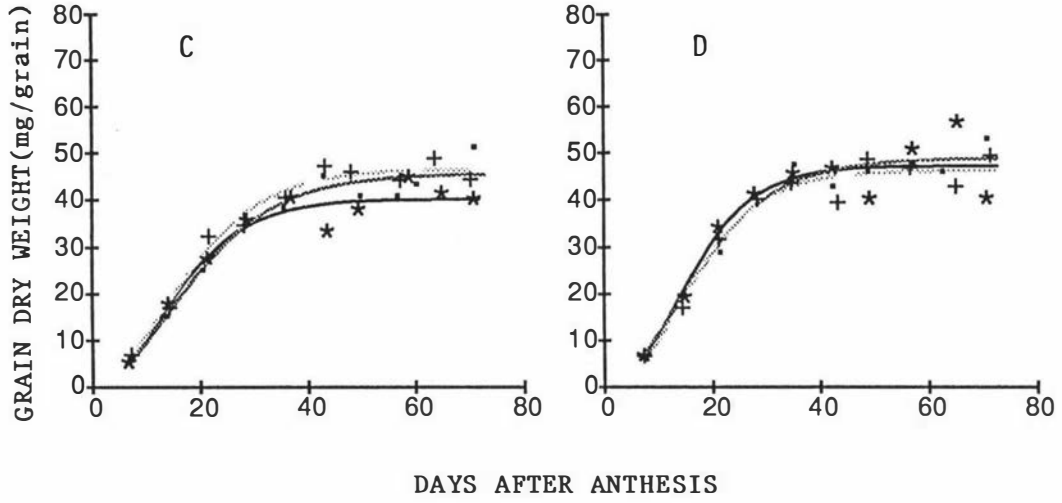
\+ observed values in block 3.

——— predicted values in block 1.

——— predicted values in block 2.

···· ····· predicted values in block 3.


A
B
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS


C
D
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS

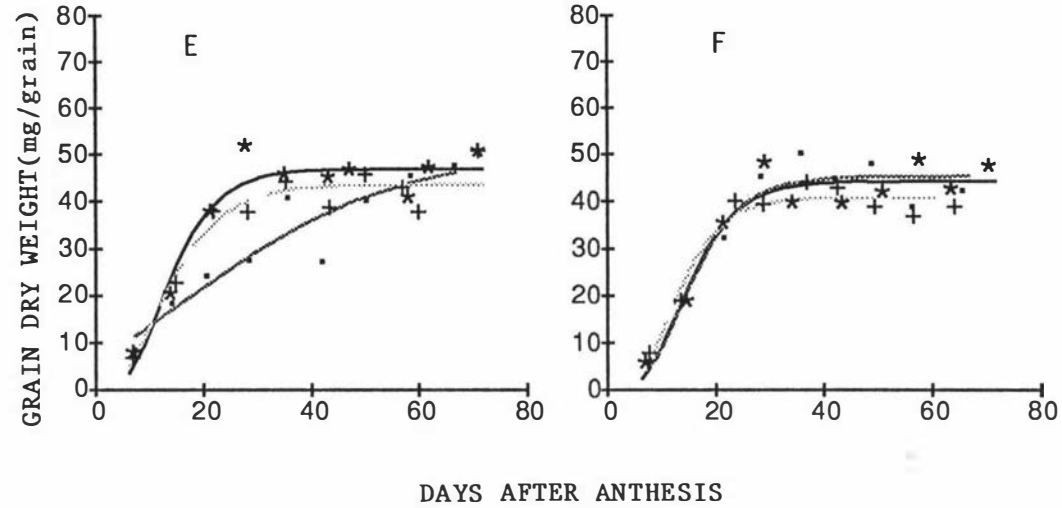

E
F
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.20. Change in grain dry weight during grain development of the six generations of cross 1 wheat ripening in the cool environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

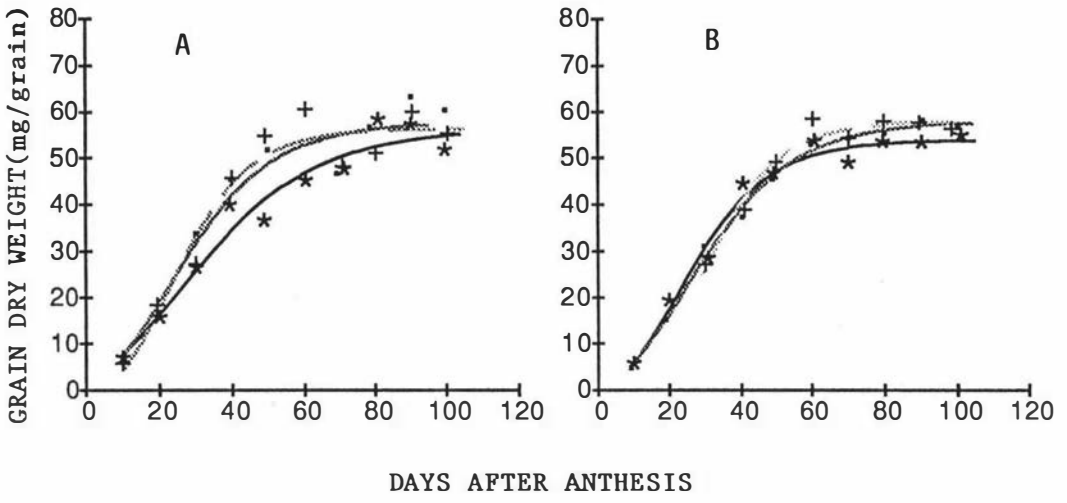
. observed values in block 2.

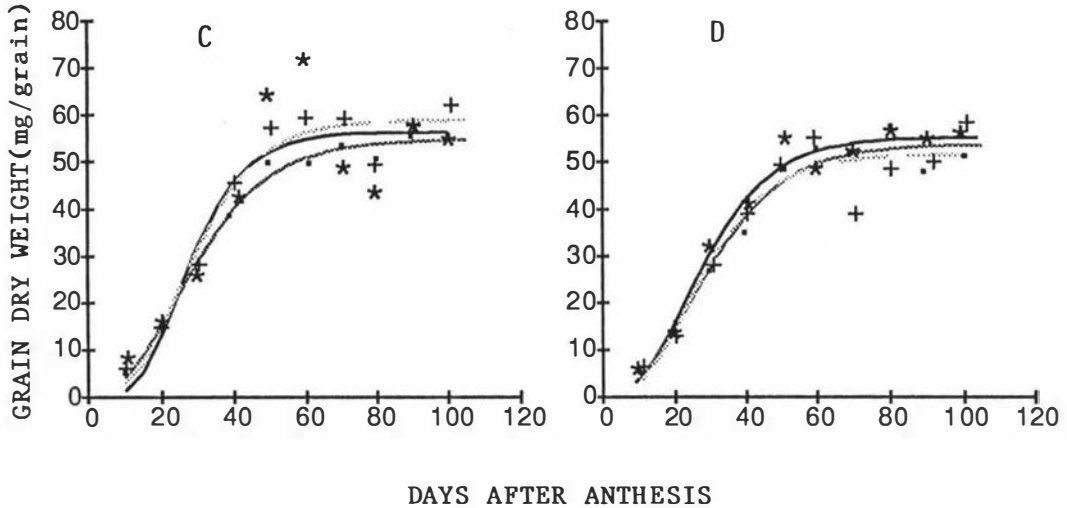
\+ observed values in block 3.

——— predicted values in block 1.

—— — predicted values in block 2.

···· ····· predicted values in block 3.


A
B
GRAIN DRY WEIGHT(mg/grain)
0 10 20 30 40 50 60 70 80
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS


C
D
GRAIN DRY WEIGHT(mg/grain)
0 10 20 30 40 50 60 70 80
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

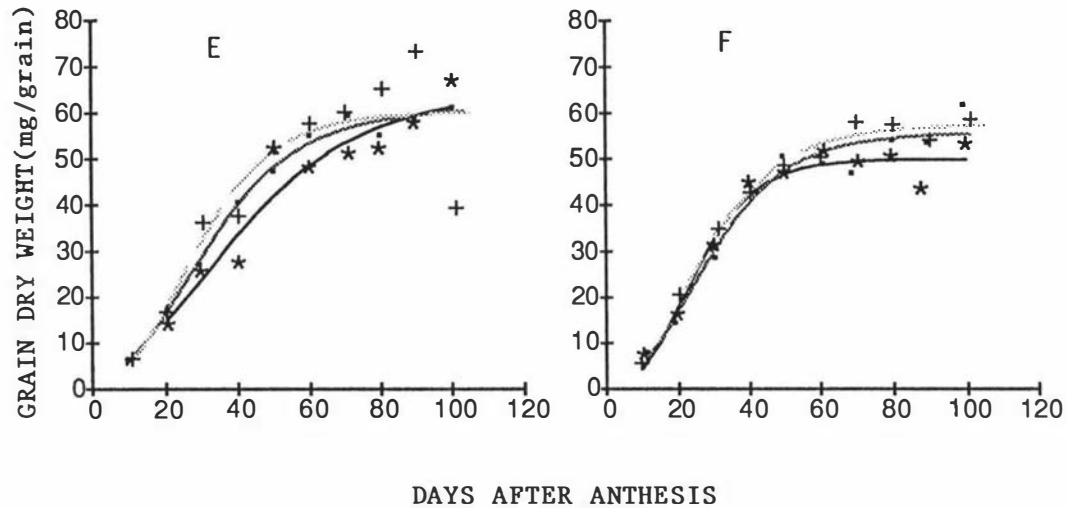

E
F
GRAIN DRY WEIGHT(mg/grain)
0 10 20 30 40 50 60 70 80
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

Figure A.21. Change in grain dry weight during grain development of the six generations of cross 2 wheat ripening in the warm environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

- - - - - - predicted values in block 2.

.... predicted values in block 3.

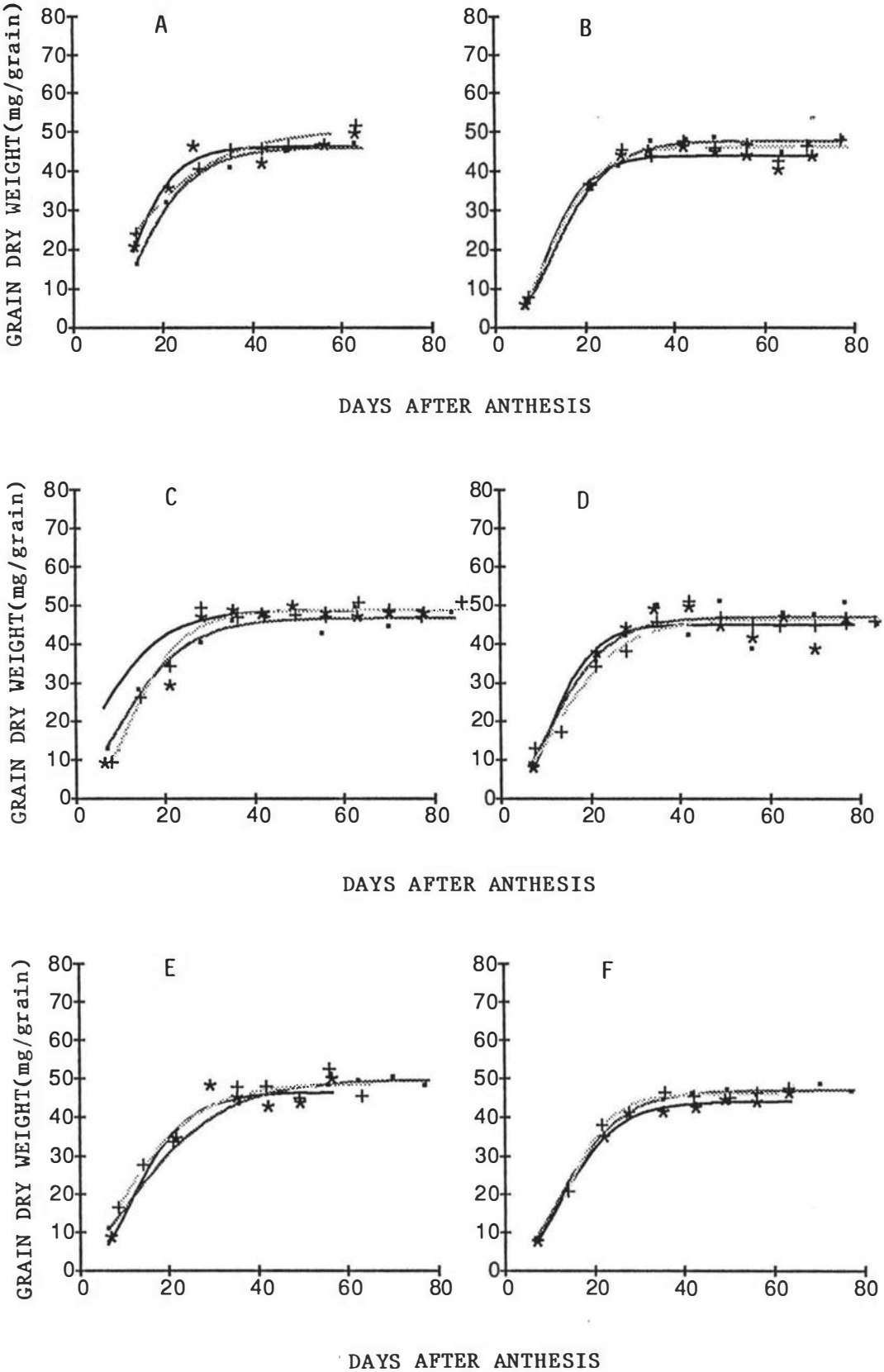

A
B
C
D
E
F
GRAIN DRY WEIGHT(mg/grain)
DAYS AFTER ANTHESIS
0
10
20
30
40
50
60
70
80

Figure A.22. Change in grain dry weight during grain development of the six generations of cross 2 wheat ripening in the cool environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

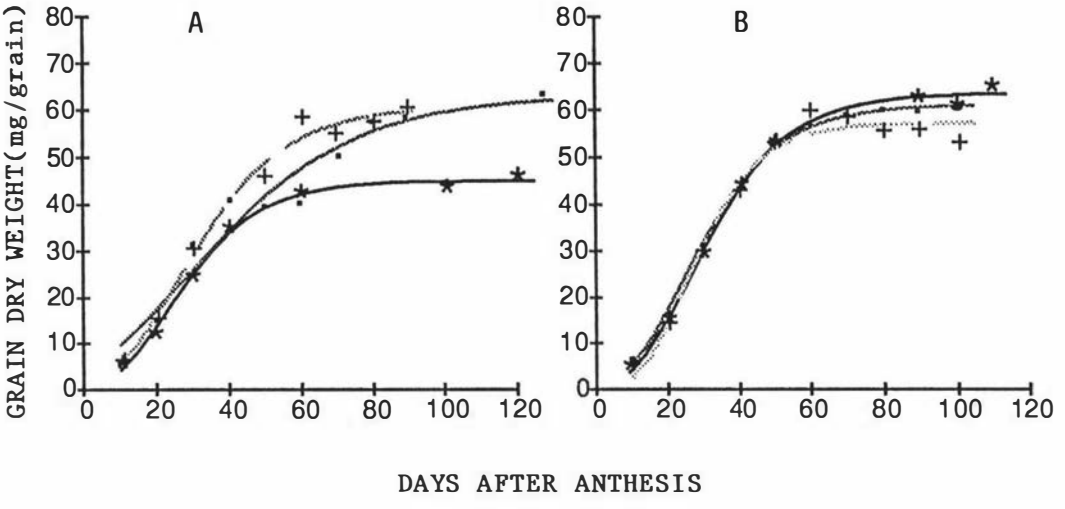
. observed values in block 2.

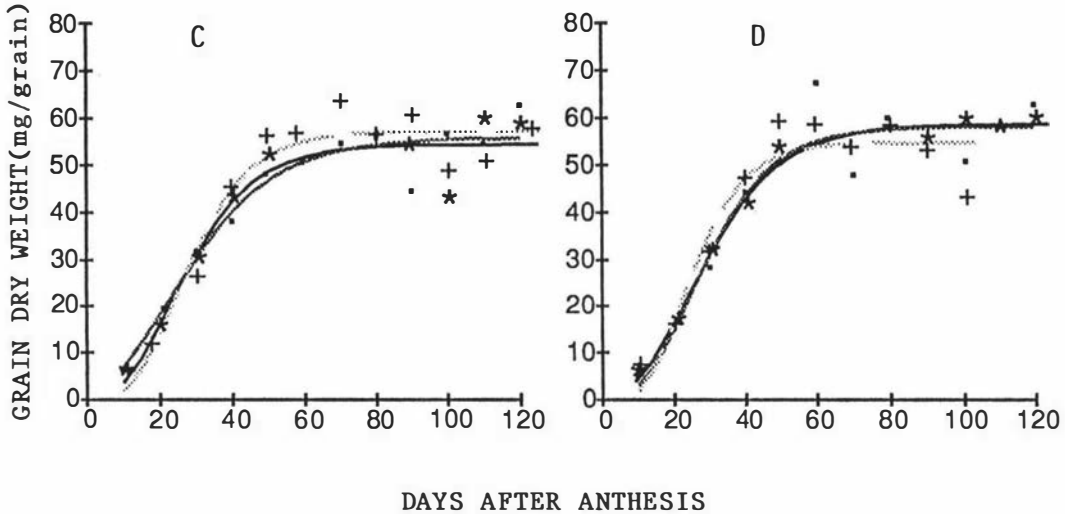
\+ observed values in block 3.

——— predicted values in block 1.

– – – – predicted values in block 2.

.... predicted values in block 3.


A
B
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS


C
D
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

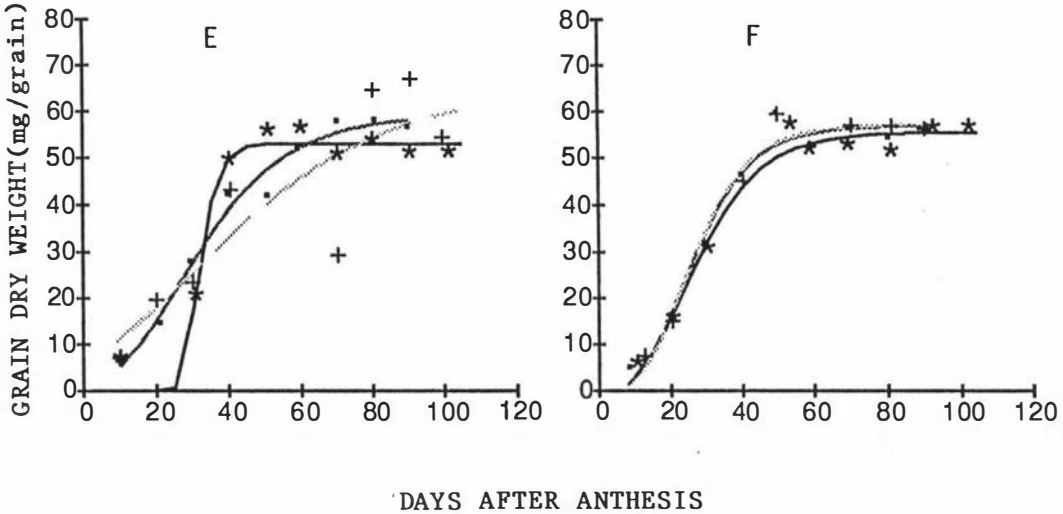

E
F
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.23. Change in grain dry weight during grain development of the six generations of cross 3 wheat ripening in the warm environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

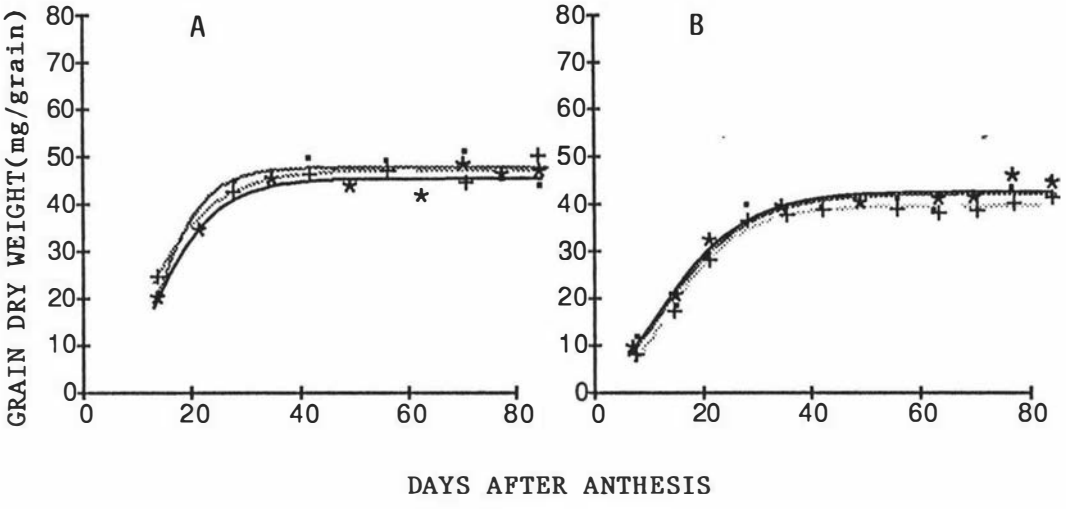
. observed values in block 2.

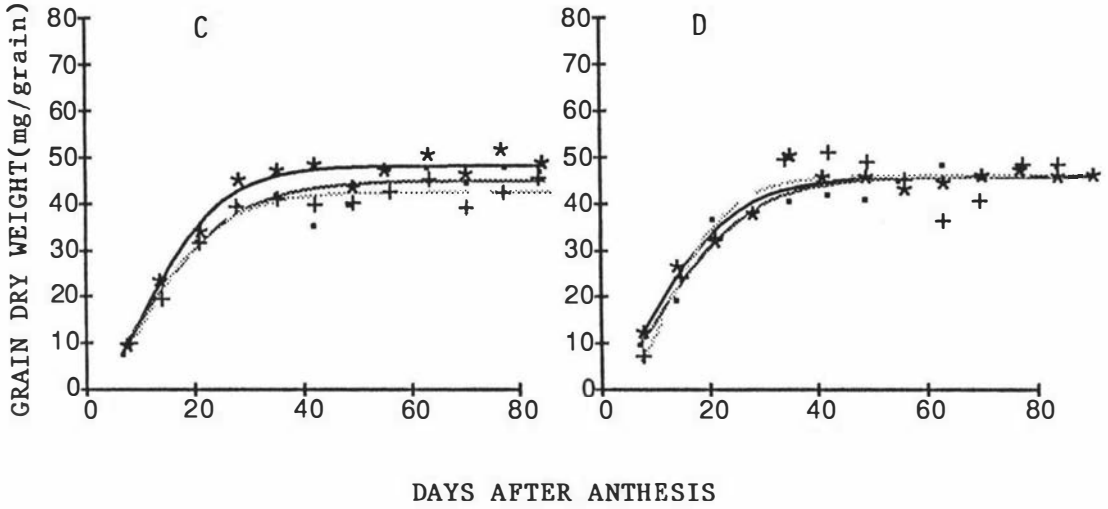
\+ observed values in block 3.

——— predicted values in block 1.

— — — predicted values in block 2.

···· ····· predicted values in block 3.


A
B
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS


C
D
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS

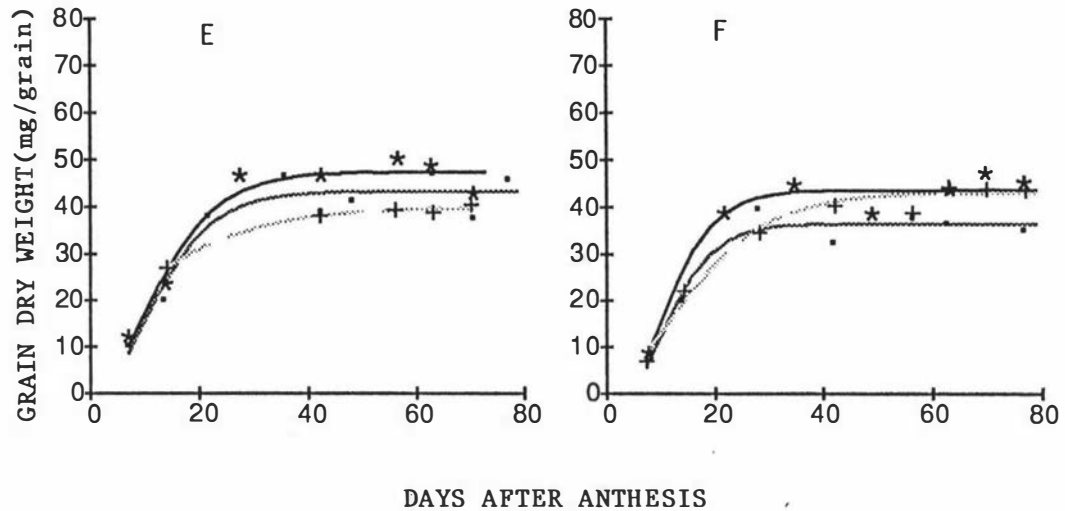

E
F
GRAIN DRY WEIGHT(mg/grain)
0
10
20
30
40
50
60
70
80
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.24. Change in grain dry weight during grain development of the six generations of cross 3 wheat ripening in the cool environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

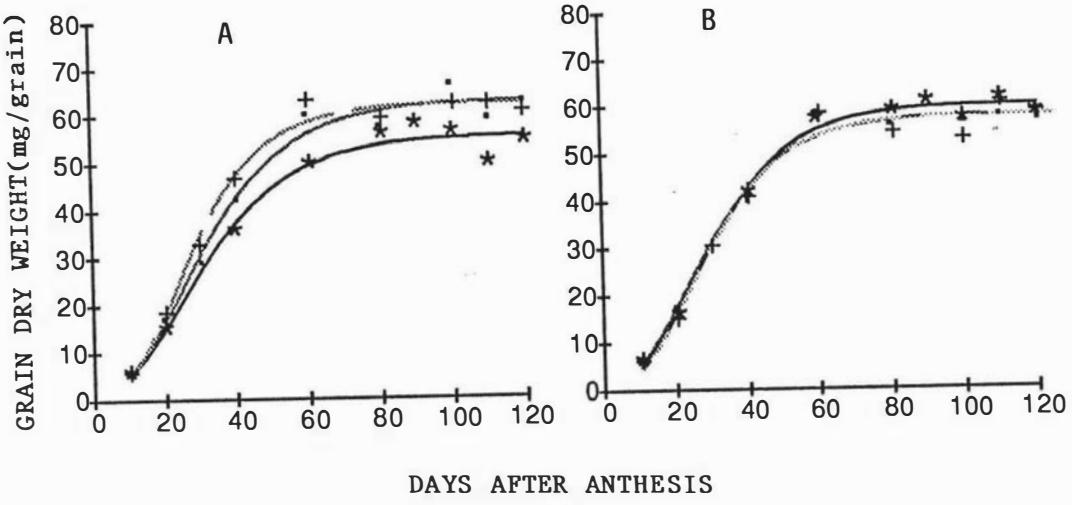
. observed values in block 2.

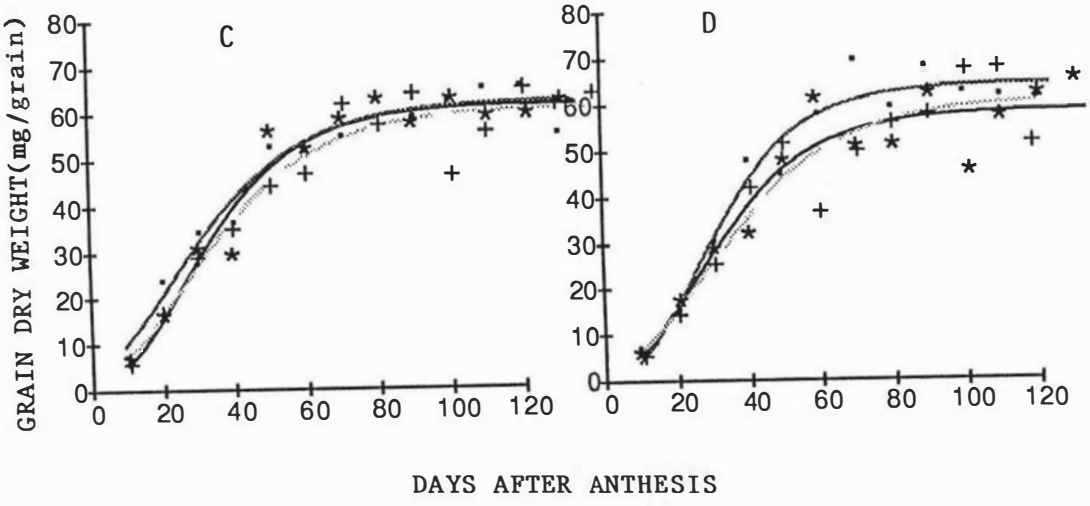
\+ observed values in block 3.

——— predicted values in block 1.

– – – – – predicted values in block 2.

···· ····· predicted values in block 3.


A
B
GRAIN DRY WEIGHT(mg/grain)
0 10 20 30 40 50 60 70 80
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS


C
D
GRAIN DRY WEIGHT(mg/grain)
0 10 20 30 40 50 60 70 80
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

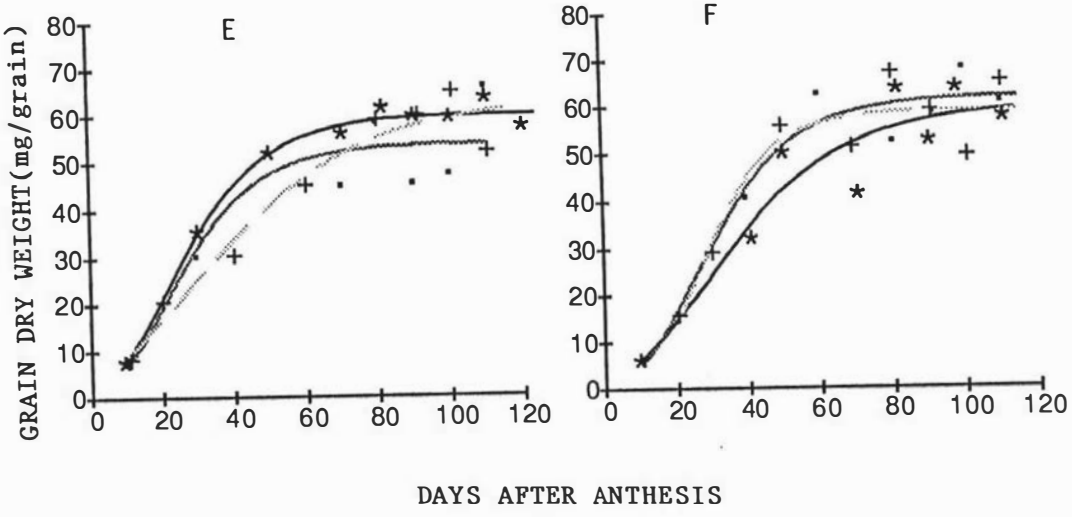

E
F
GRAIN DRY WEIGHT(mg/grain)
0 10 20 30 40 50 60 70 80
0 20 40 60 80 100 120
DAYS AFTER ANTHESIS

Figure A.25. Change in base a-amylase during grain development of the six generations of cross 1 wheat ripening in the warm environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

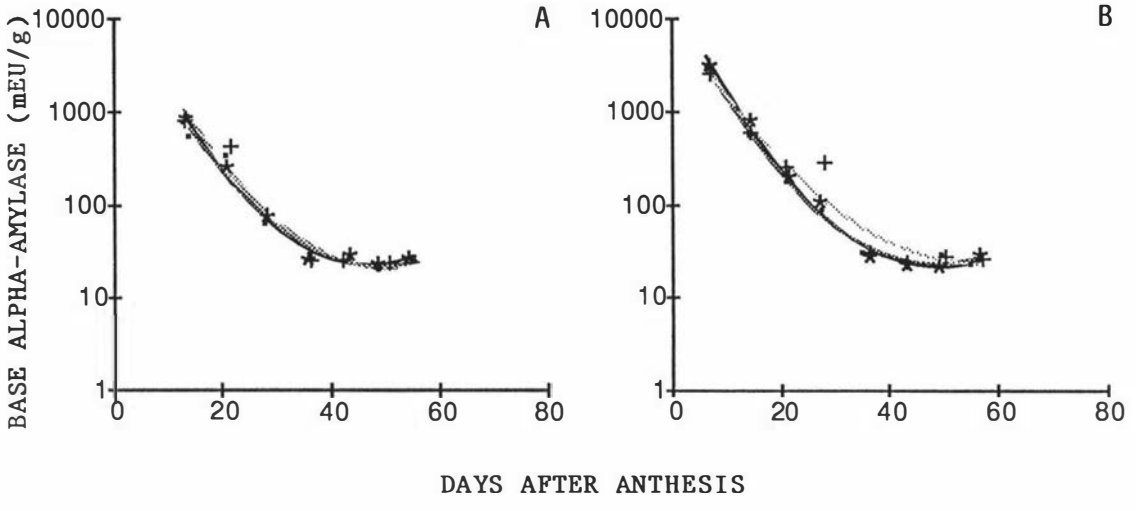
. observed values in block 2.

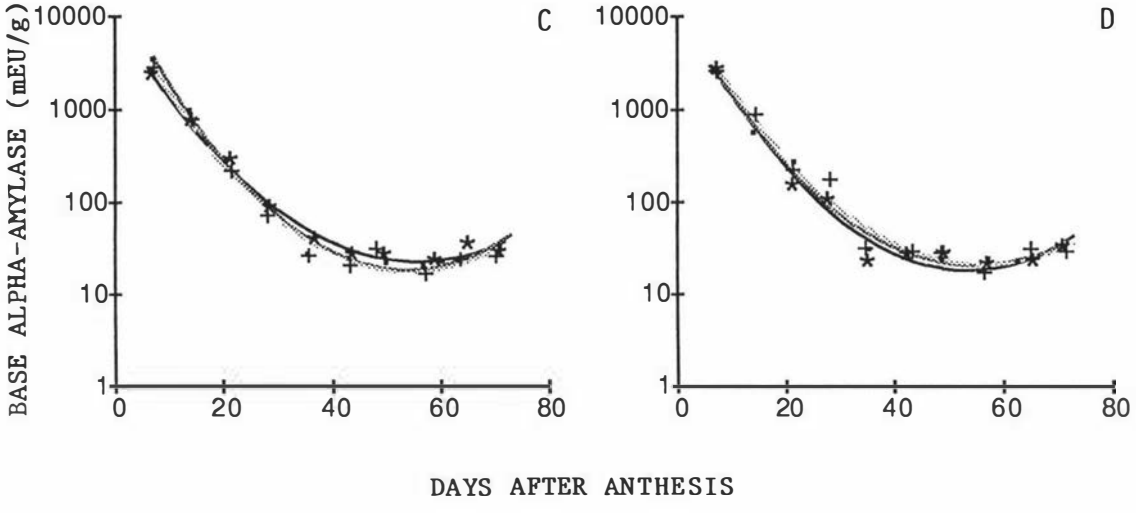
\+ observed values in block 3.

——— predicted values in block 1.

- - - - - - - - - predicted values in block 2.

···· ····· predicted values in block 3.


A
B
BASE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS


C
D
BASE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS

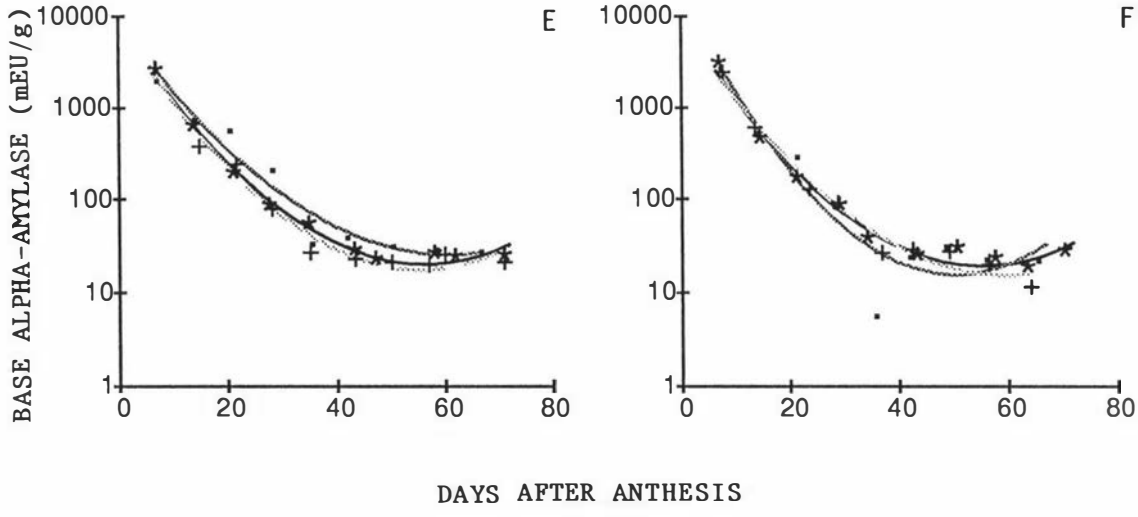

E
F
BASE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.26. Change in base a-amylase during grain development of the six generations of cross 1 wheat ripening in the cool environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

———- predicted values in block 2.

···· ····· predicted values in block 3.

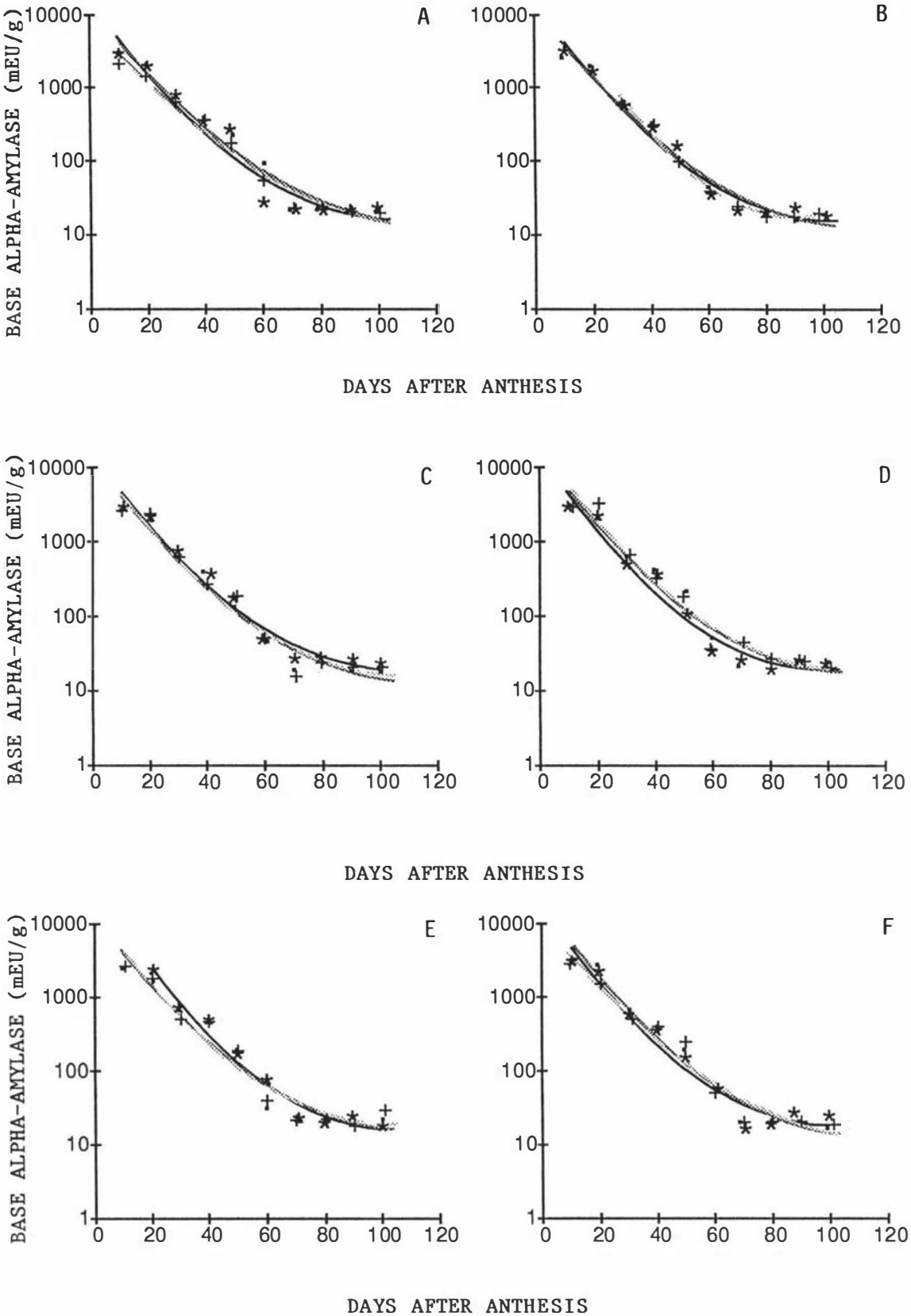

A
B
C
D
E
F
BASE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.27. Change in germinative a-amylase during grain development of the six generations of cross 1 wheat ripening in the warm environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : $BC_1(Tordo)S_1$

F : $BC_1(Karamu)S_1$

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

– – – – – predicted values in block 2.

.... predicted values in block 3.

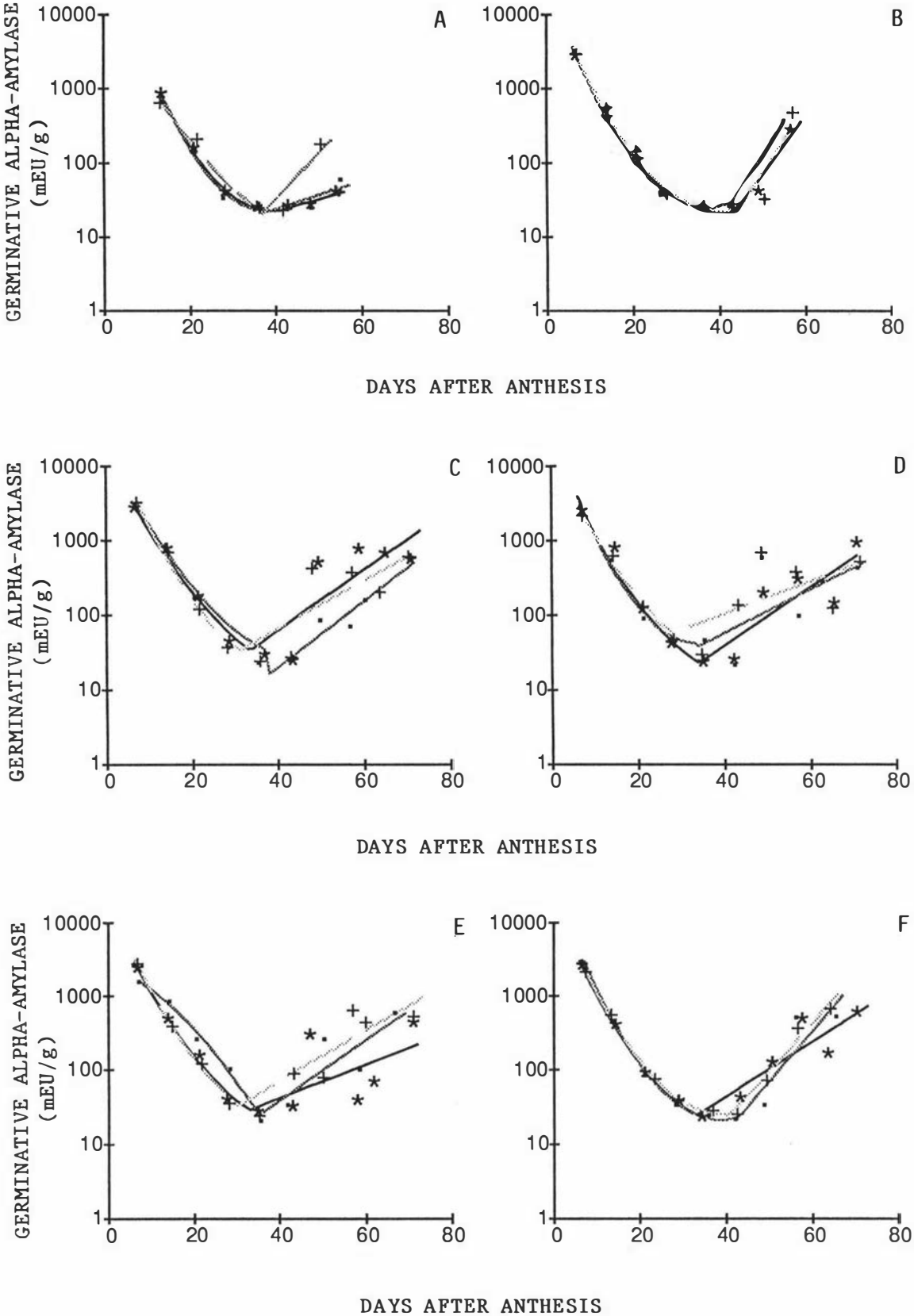

GERMINATIVE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
A
B
C
D
E
F
DAYS AFTER ANTHESIS

Figure A.28. Change in germinative a-amylase during grain development of the six generations of cross 1 wheat ripening in the cool environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

_____ predicted values in block 1.

_____ predicted values in block 2.

.... predicted values in block 3.

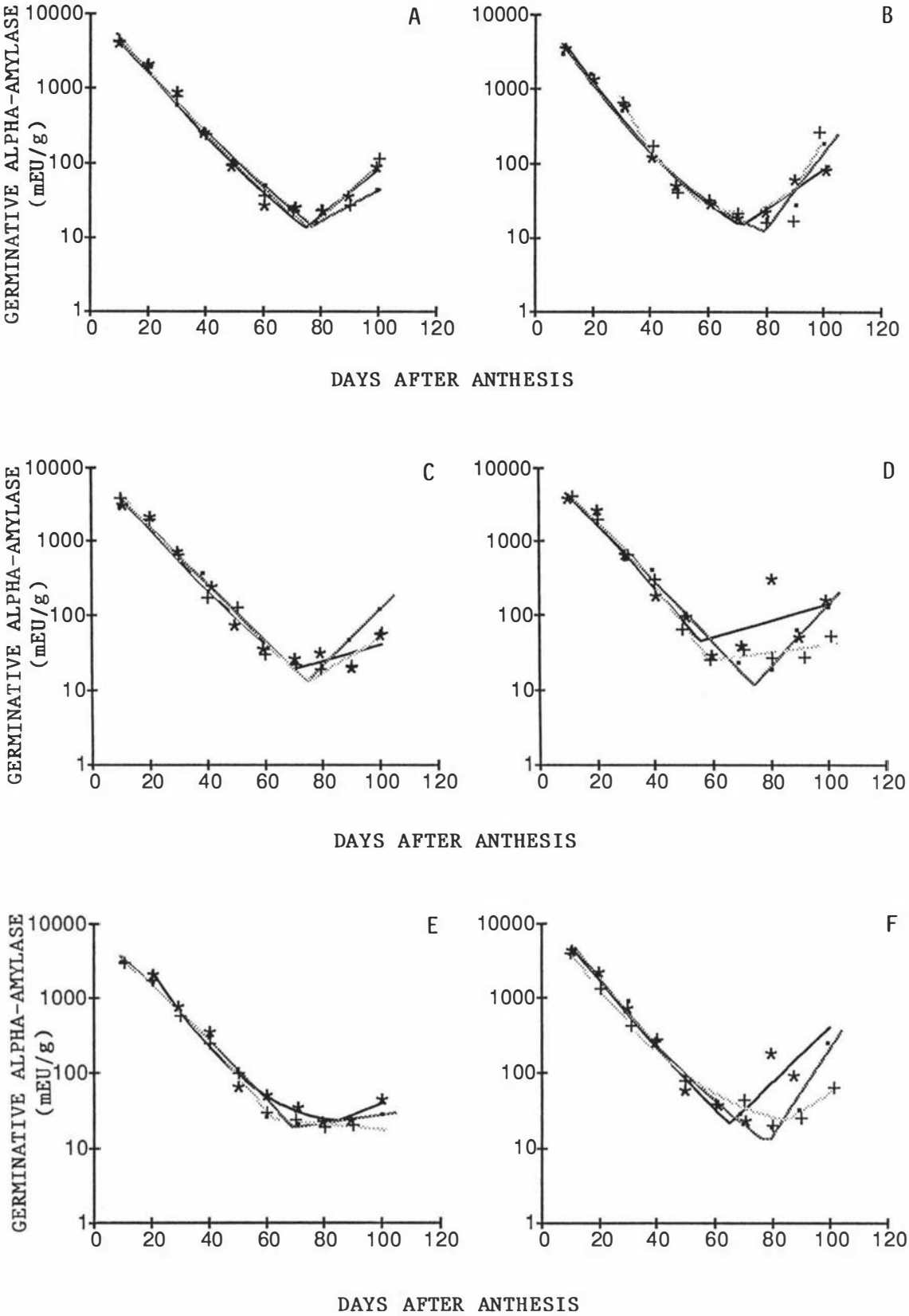

A
B
C
D
E
F
GERMINATIVE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.29. Change in GA_3 a-amylase during grain development of the six generations of cross 1 wheat ripening in the warm environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

——— predicted values in block 2.

.... predicted values in block 3.

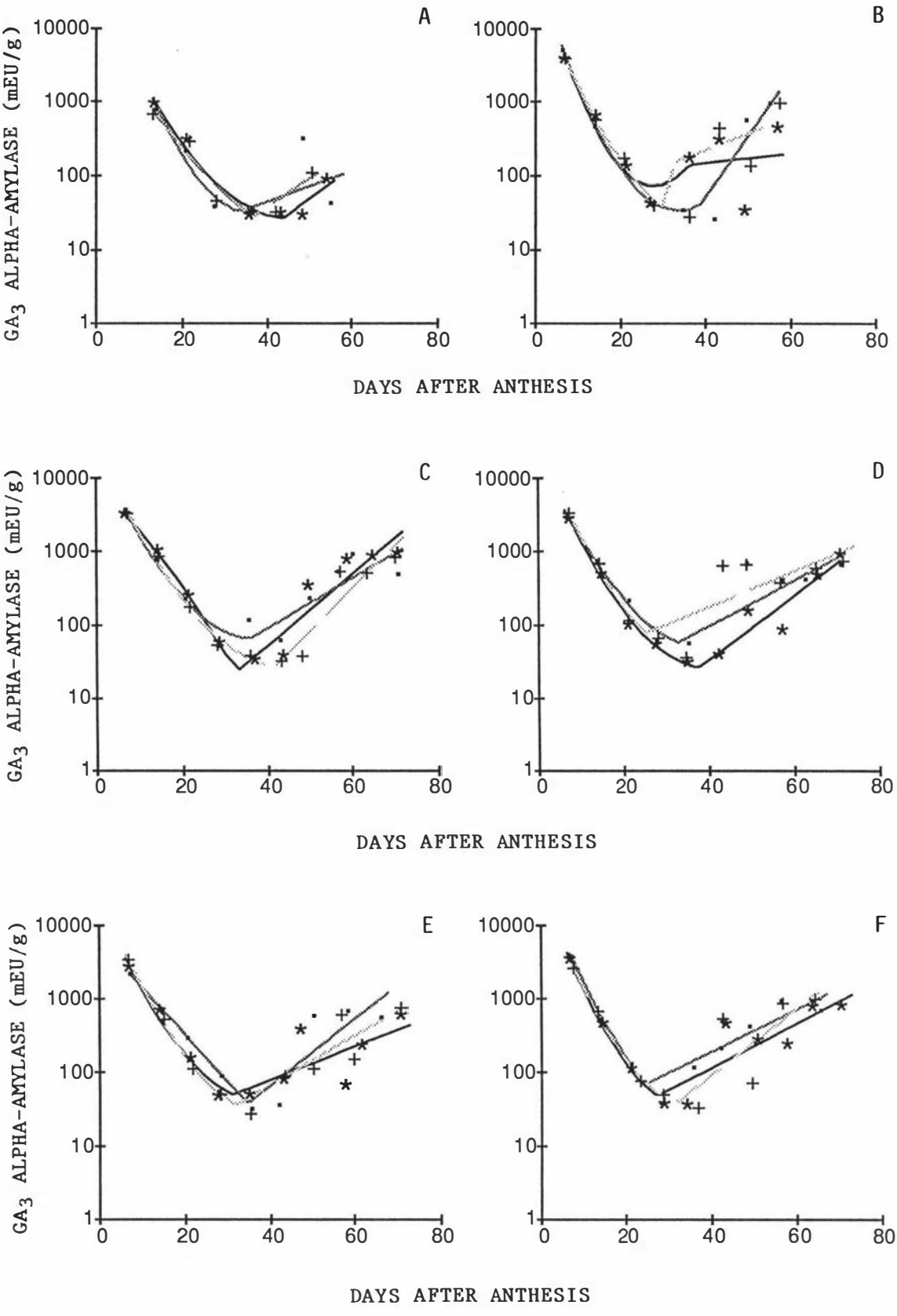

A
B
C
D
E
F
GA3 ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.30. Change in GA_3 a-amylase during grain development of the six generations of cross 1 wheat ripening in the cool environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

predicted values in block 1.

predicted values in block 2.

predicted values in block 3.

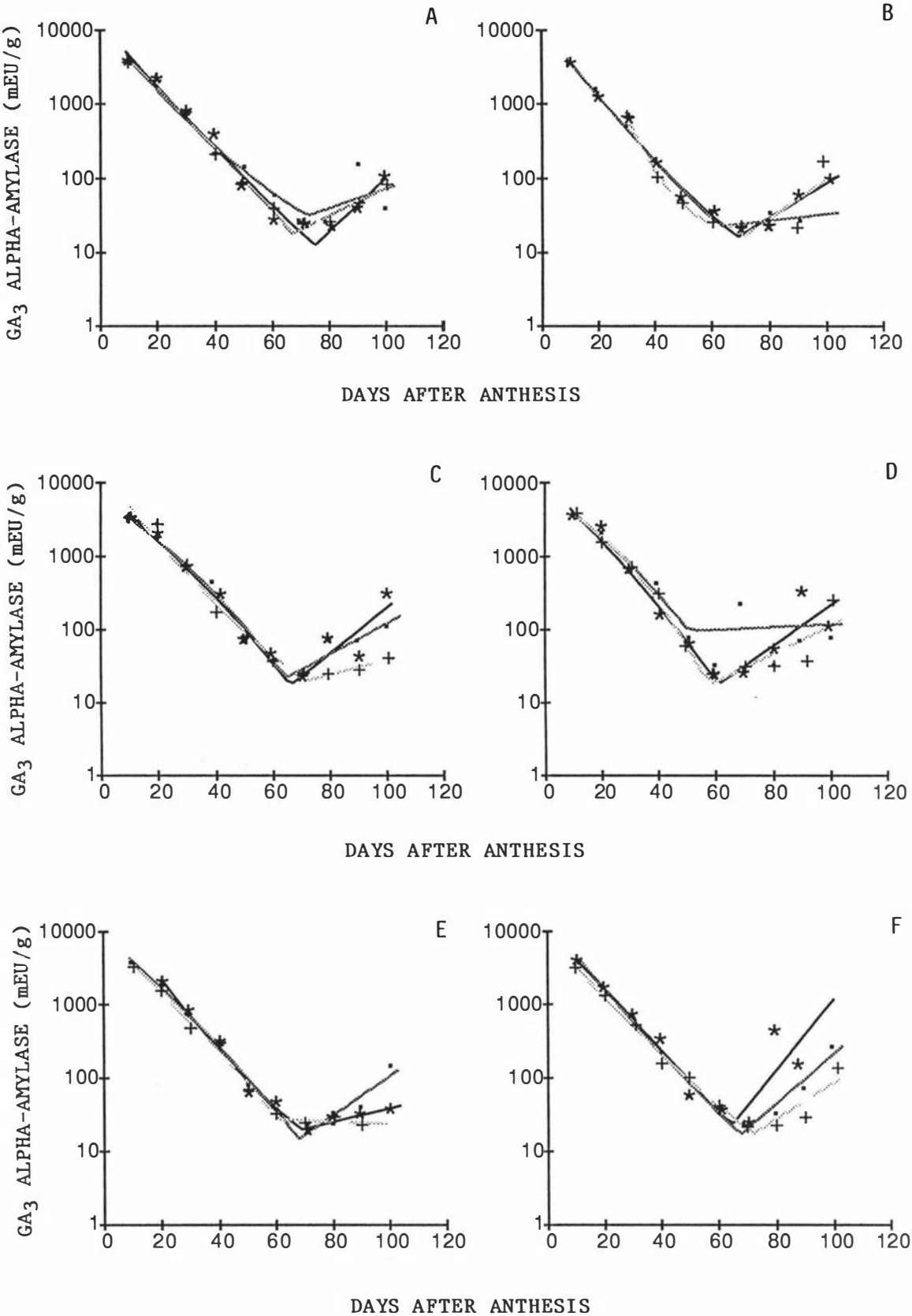

A
B
C
D
E
F
GA3 ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.31. Change in base a-amylase during grain development of the six generations of cross 2 wheat ripening in the warm environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

predicted values in block 1.

predicted values in block 2.

predicted values in block 3.

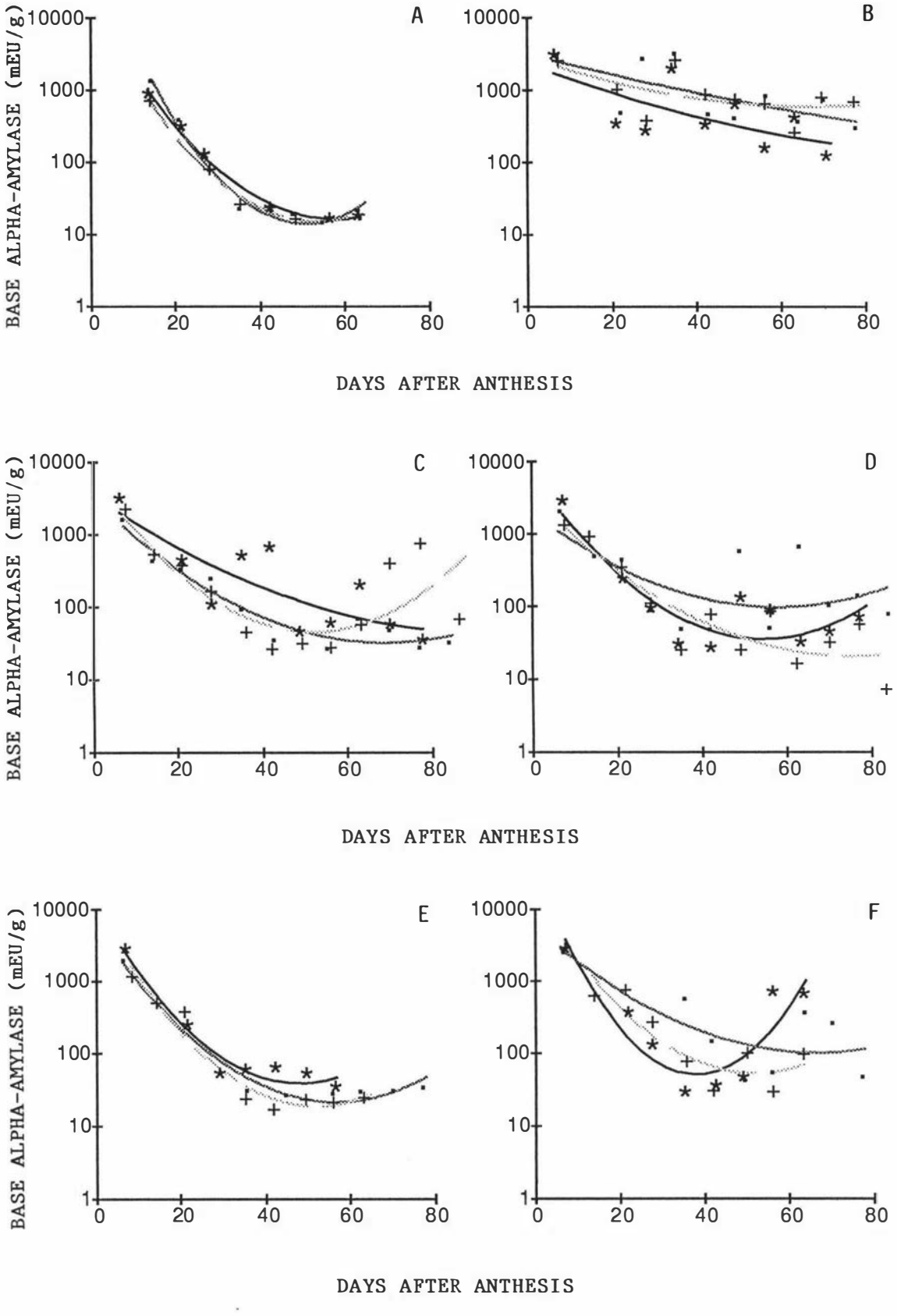

A
B
C
D
E
F
BASE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.32. Change in base a-amylase during grain development of the six generations of cross 2 wheat ripening in the cool environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

– – – – – predicted values in block 2.

···· ····· predicted values in block 3.

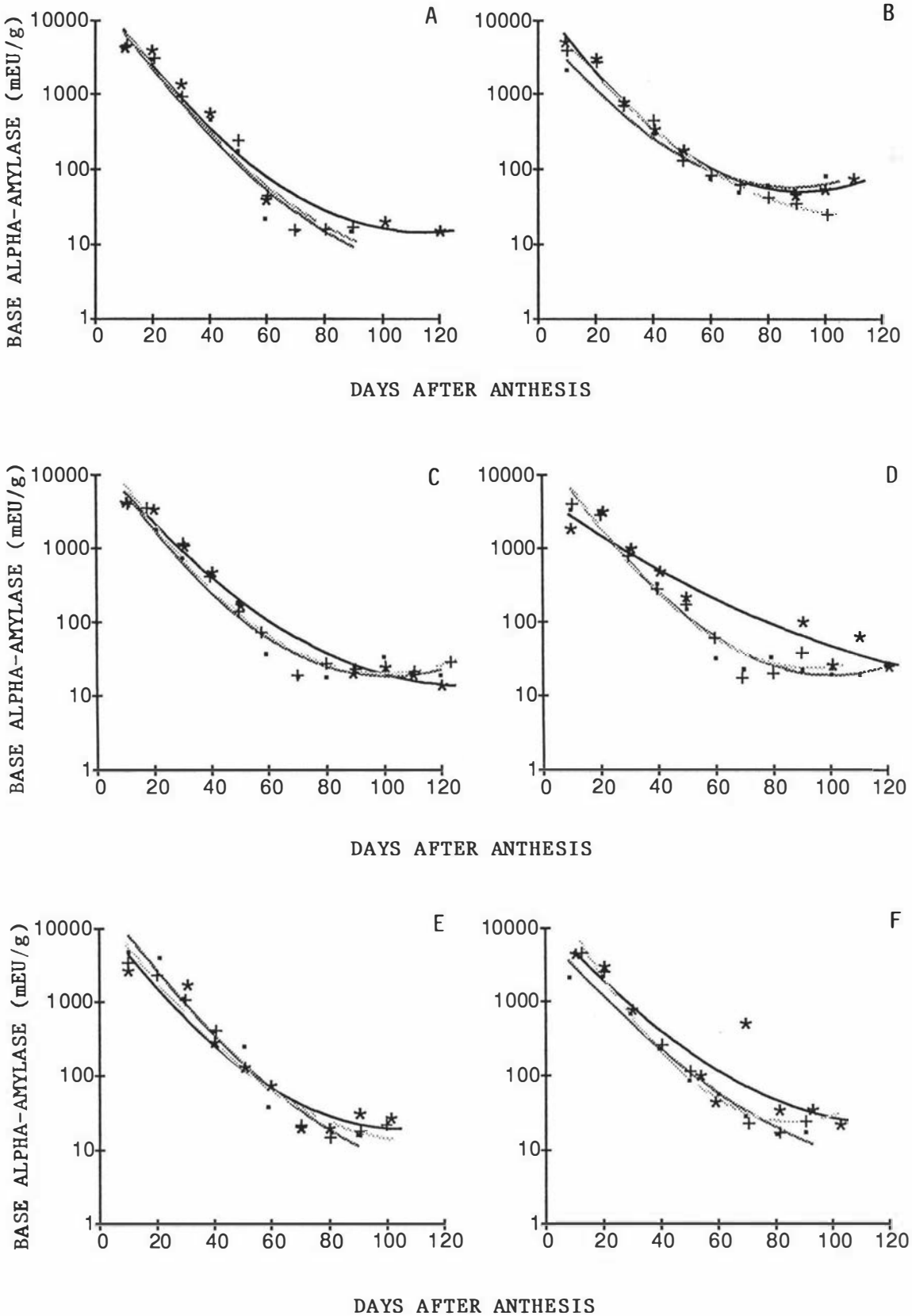

A
B
C
D
E
F
BASE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.33. Change in germinative a-amylase during grain development of the six generations of cross 2 wheat ripening in the warm environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

. observed values in block 2.

+ observed values in block 3.

——— predicted values in block 1.

– – – – predicted values in block 2.

···· ····· predicted values in block 3.

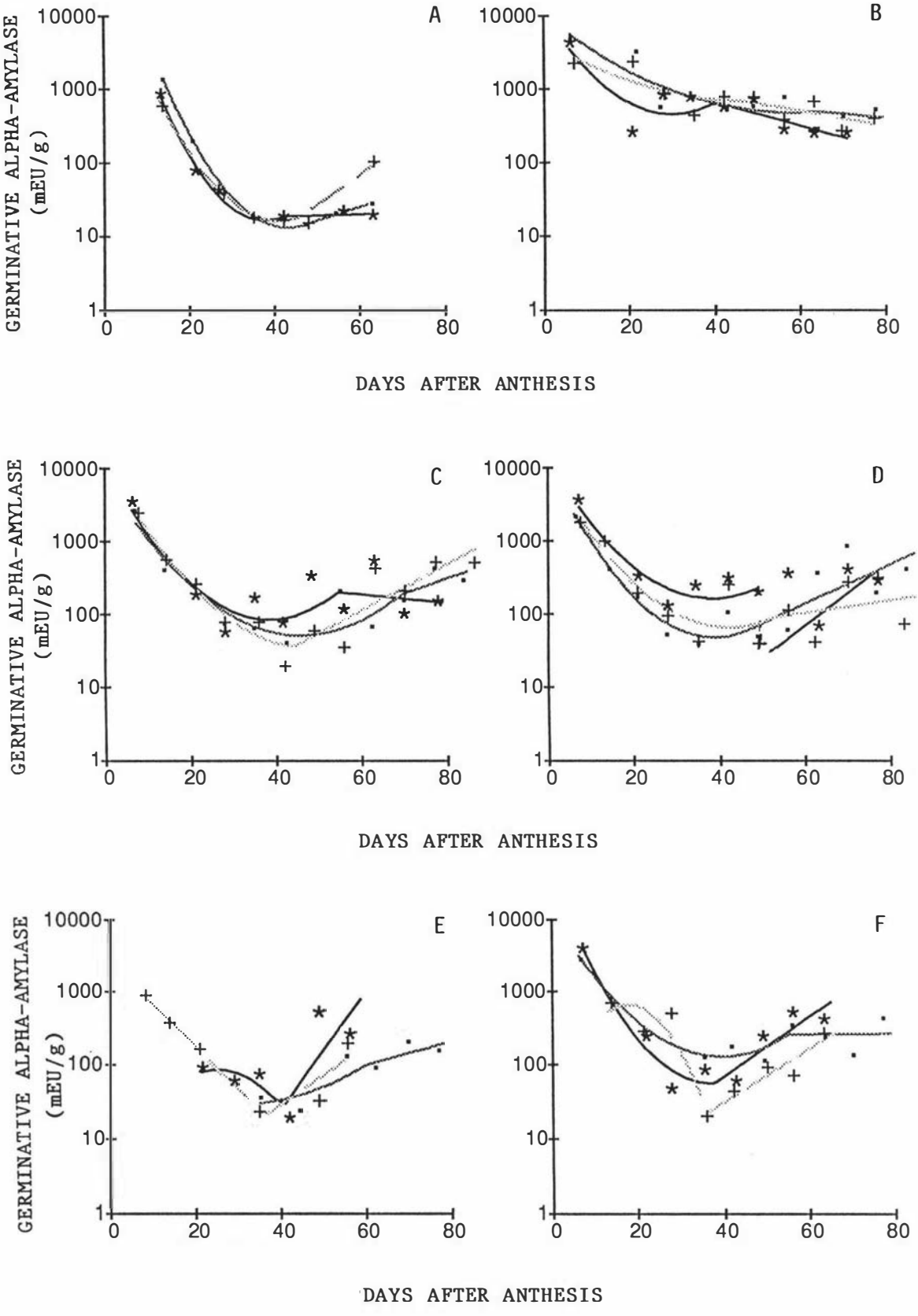

A
B
C
D
E
F
GERMINATIVE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.34. Change in germinative a-amylase during grain development of the six generations of cross 2 wheat ripening in the cool environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1 (Tordo) S_1

F : BC_1 (Gabo) S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

_____ predicted values in block 1.

_ _ _ _ _ predicted values in block 2.

.... predicted values in block 3.

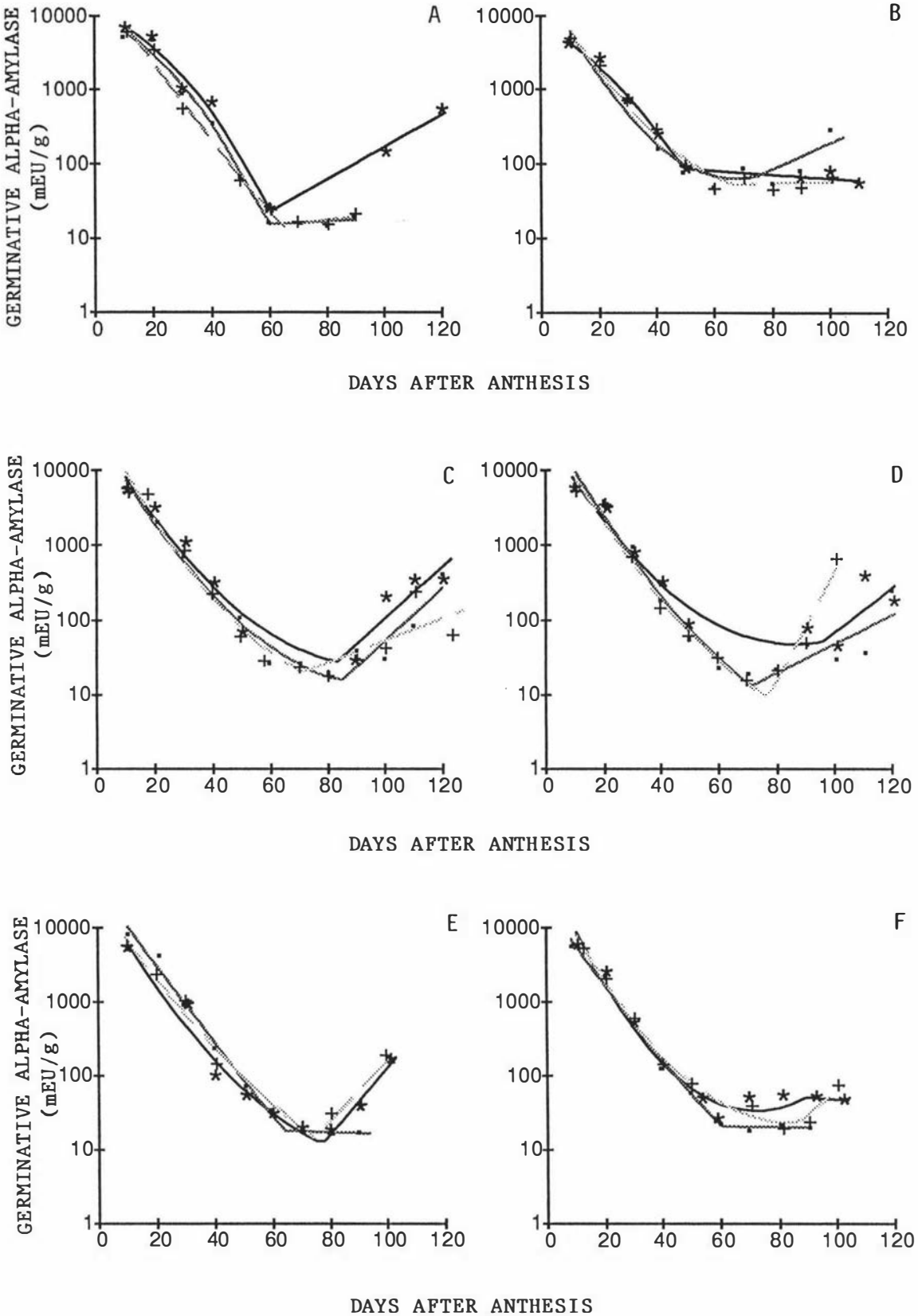

A
B
C
D
E
F
GERMINATIVE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.35. Change in GA_3 a-amylase during grain development of the six generations of cross 2 wheat ripening in the warm environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : $BC_1(Tordo)S_1$

F : $BC_1(Gabo)S_1$

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

_____ predicted values in block 1.

_ _ _ _ _ predicted values in block 2.

.... predicted values in block 3.

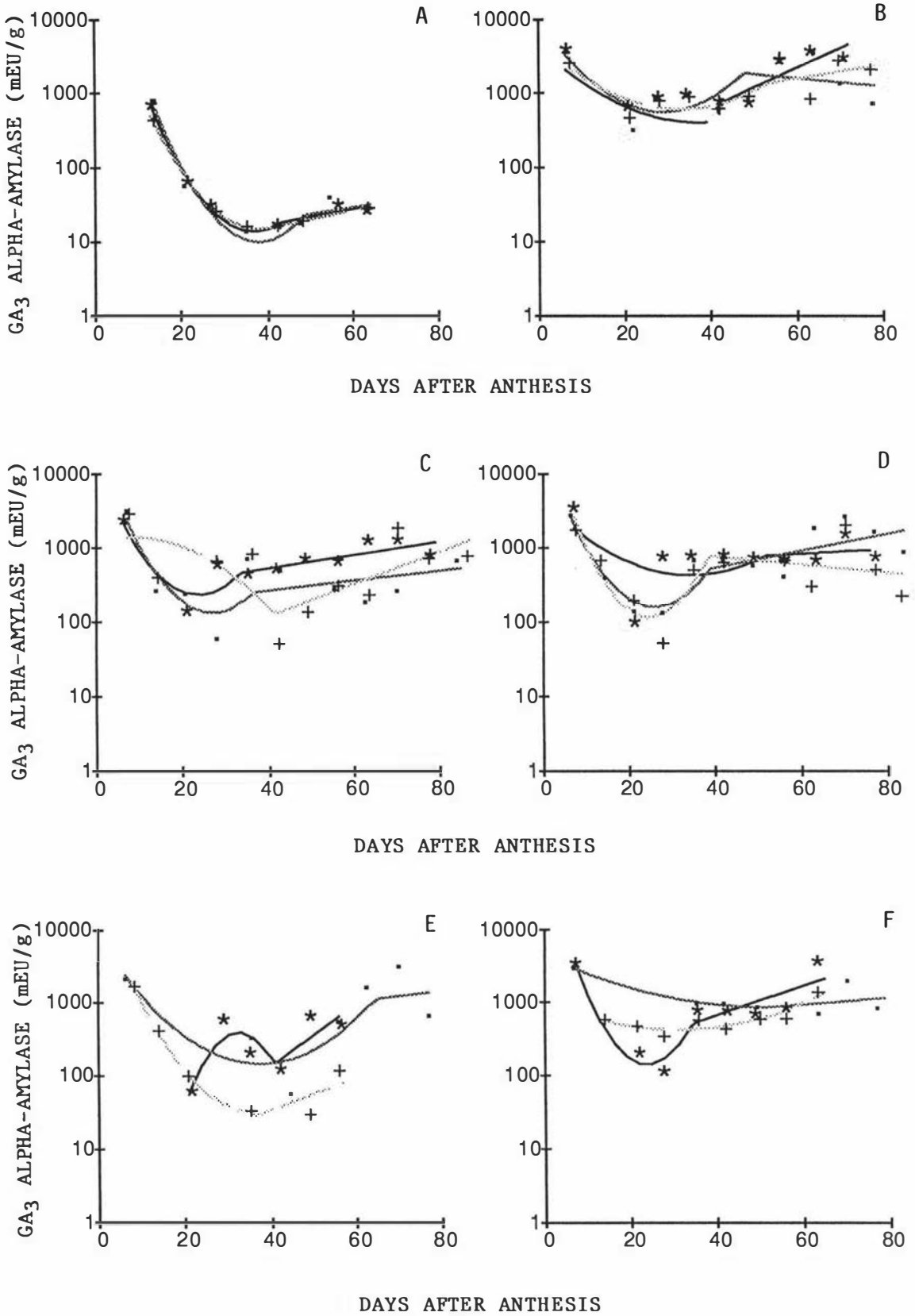

A
B
C
D
E
F
GA3 ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.36. Change in GA_3 a-amylase during grain development of the six generations of cross 2 wheat ripening in the cool environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

- - - - - - - - predicted values in block 2.

.... predicted values in block 3.

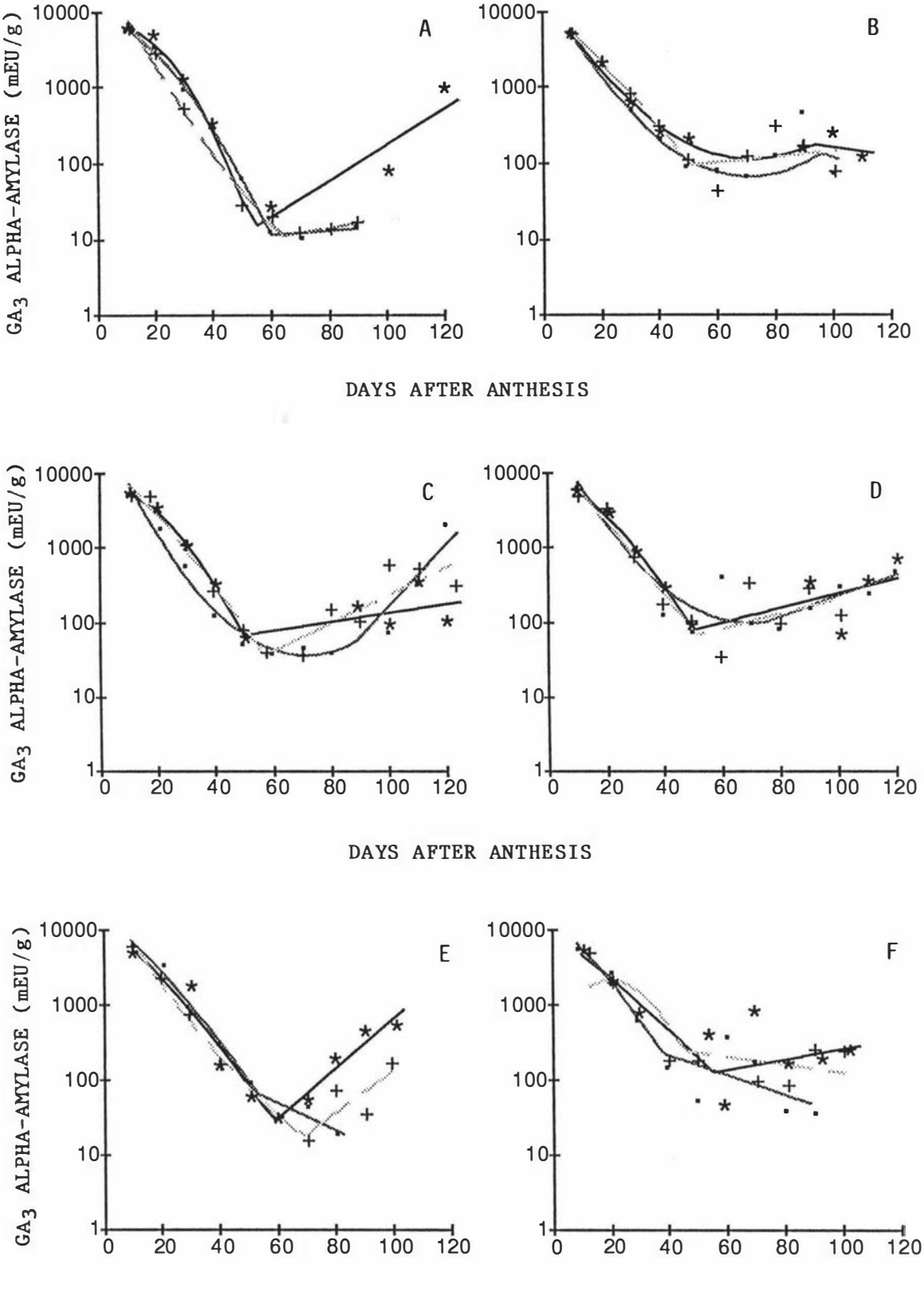

A
B
C
D
E
F
GA3 ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.37. Change in base a-amylase during grain development of the six generations of cross 3 wheat ripening in the warm environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

— — — — predicted values in block 2.

.... predicted values in block 3.

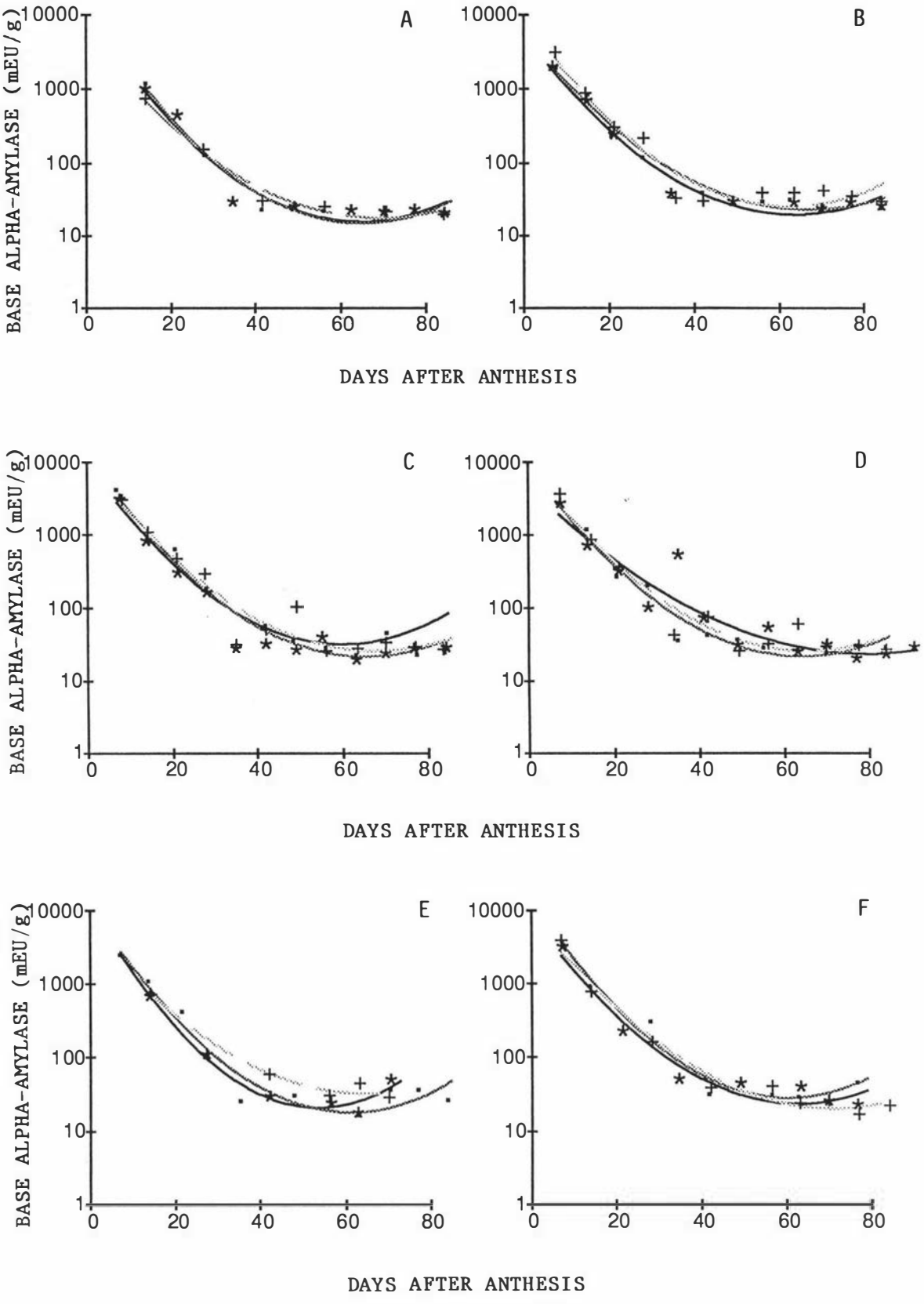

A
B
C
D
E
F
BASE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.38. Change in base a-amylase during grain development of the six generations of cross 3 wheat ripening in the cool environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

_____ predicted values in block 2.

.... predicted values in block 3.

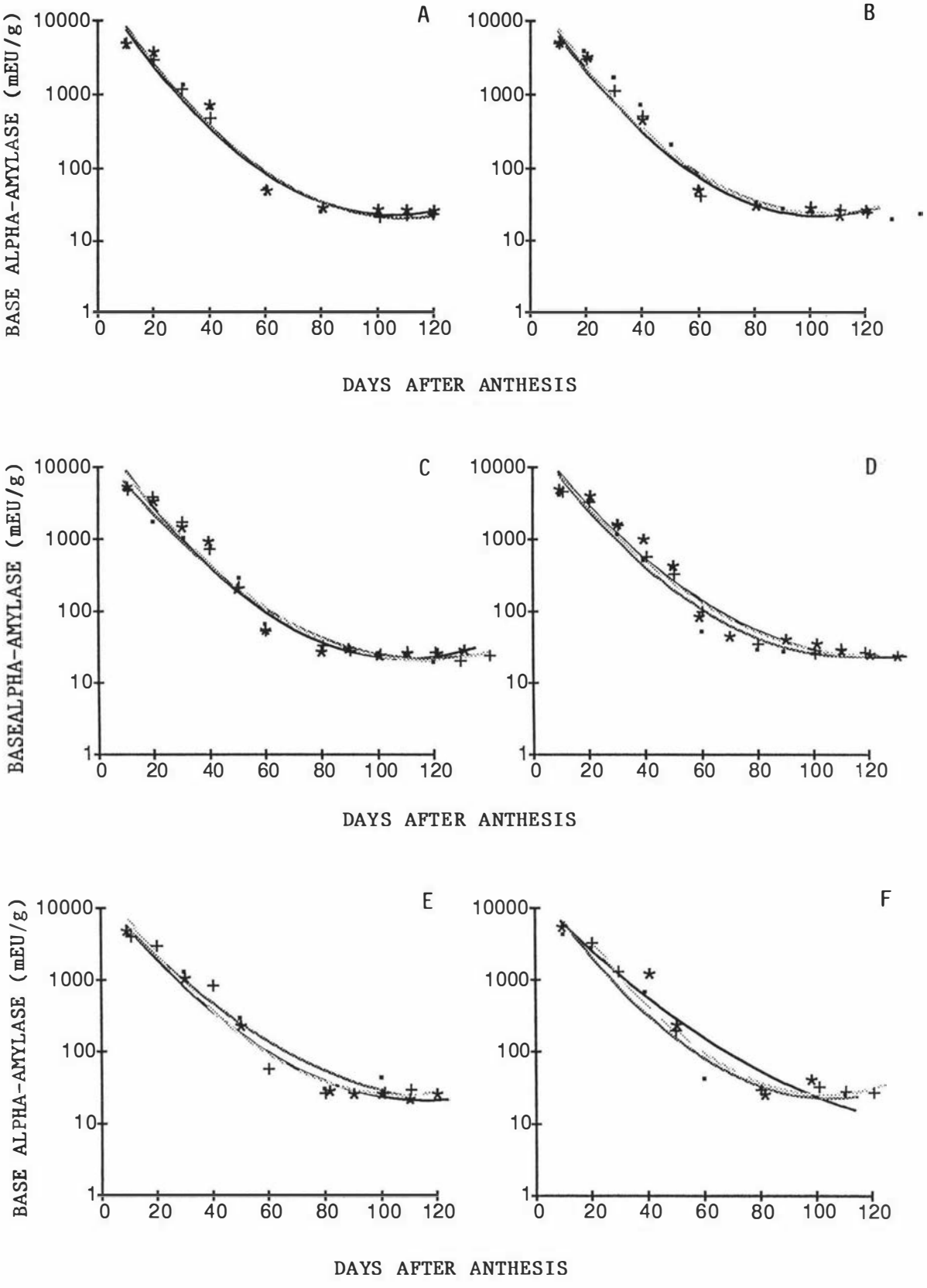

A
B
C
D
E
F
BASE ALPHA-AMYLASE (mEU/g)
BASEALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.39. Change in germinative a-amylase during grain development of the six generations of cross 3 wheat ripening in the warm environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

_____ predicted values in block 1.

_ _ _ _ _ predicted values in block 2.

.... predicted values in block 3.

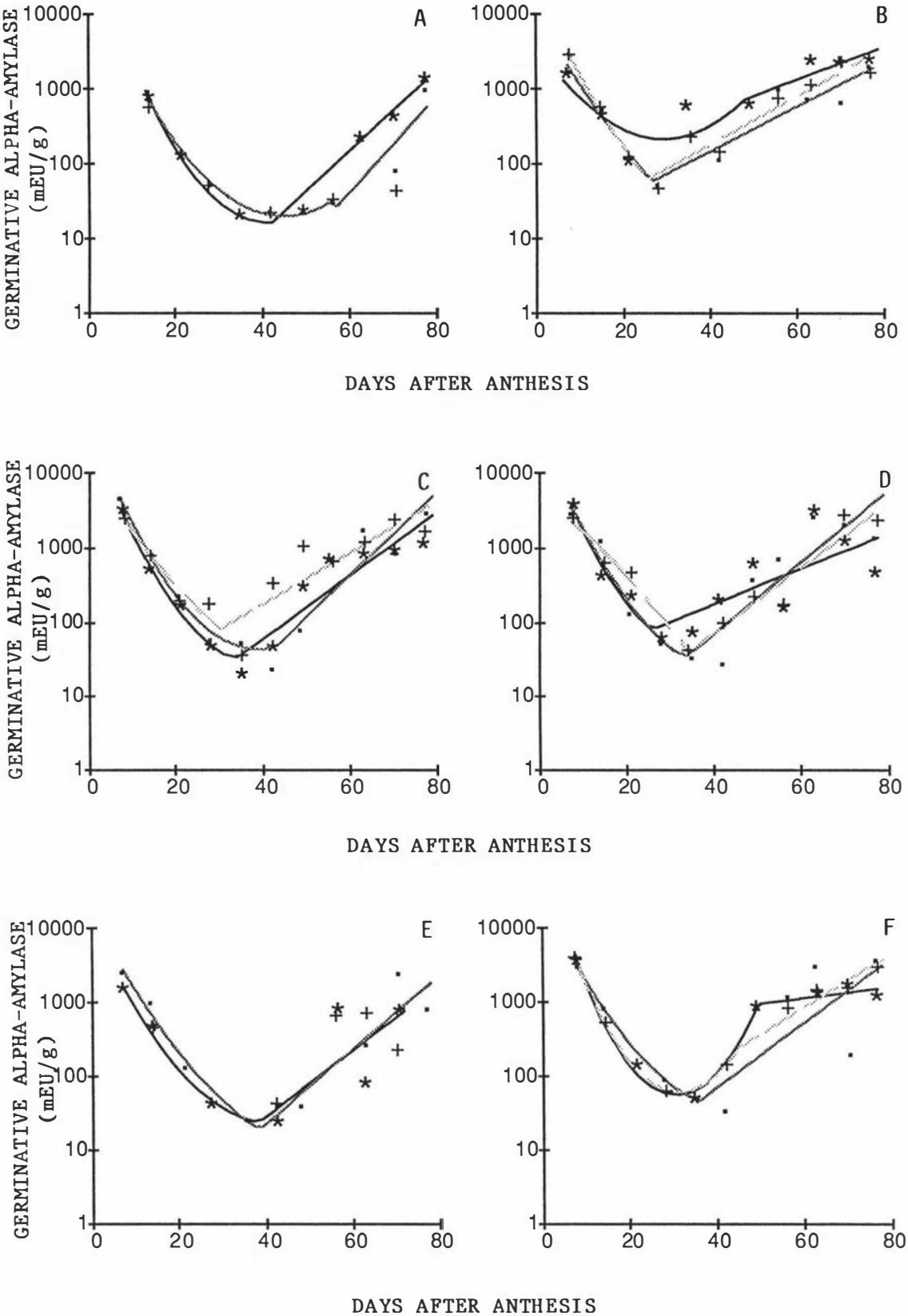

A
B
C
D
E
F
GERMINATIVE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
0
20
40
60
80
DAYS AFTER ANTHESIS

Figure A.40. Change in germinative a-amylase during grain development of the six generations of cross 3 wheat ripening in the cool environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

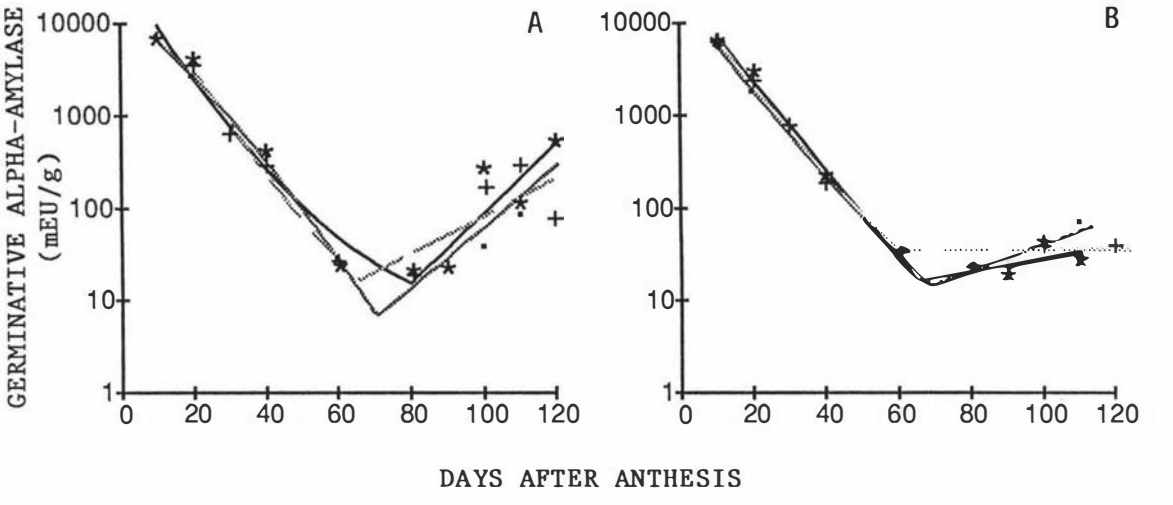
. observed values in block 2.

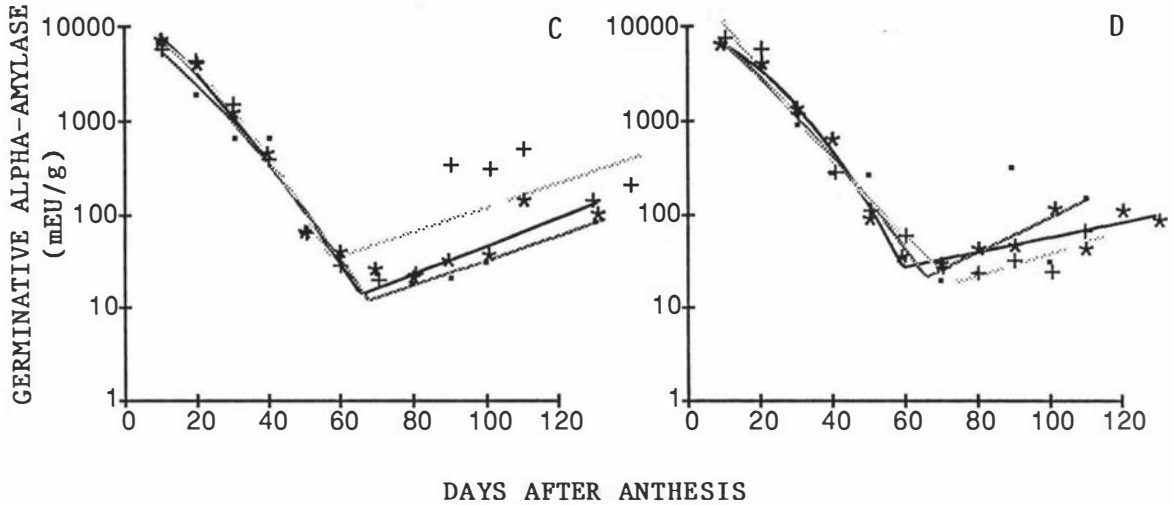
\+ observed values in block 3.

——— predicted values in block 1.

——— predicted values in block 2.

.... predicted values in block 3.


GERMINATIVE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
A
B
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS


GERMINATIVE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
C
D
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

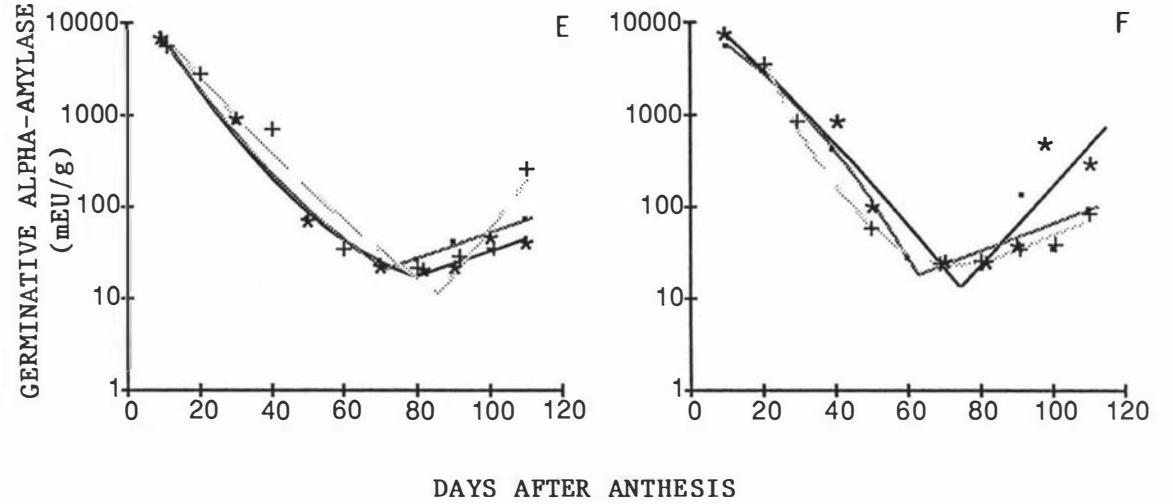

GERMINATIVE ALPHA-AMYLASE (mEU/g)
10000
1000
100
10
1
E
F
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.41. Change in GA_3 a-amylase during grain development of the six generations of cross 3 wheat ripening in the warm environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

– – – – – predicted values in block 2.

.... predicted values in block 3.

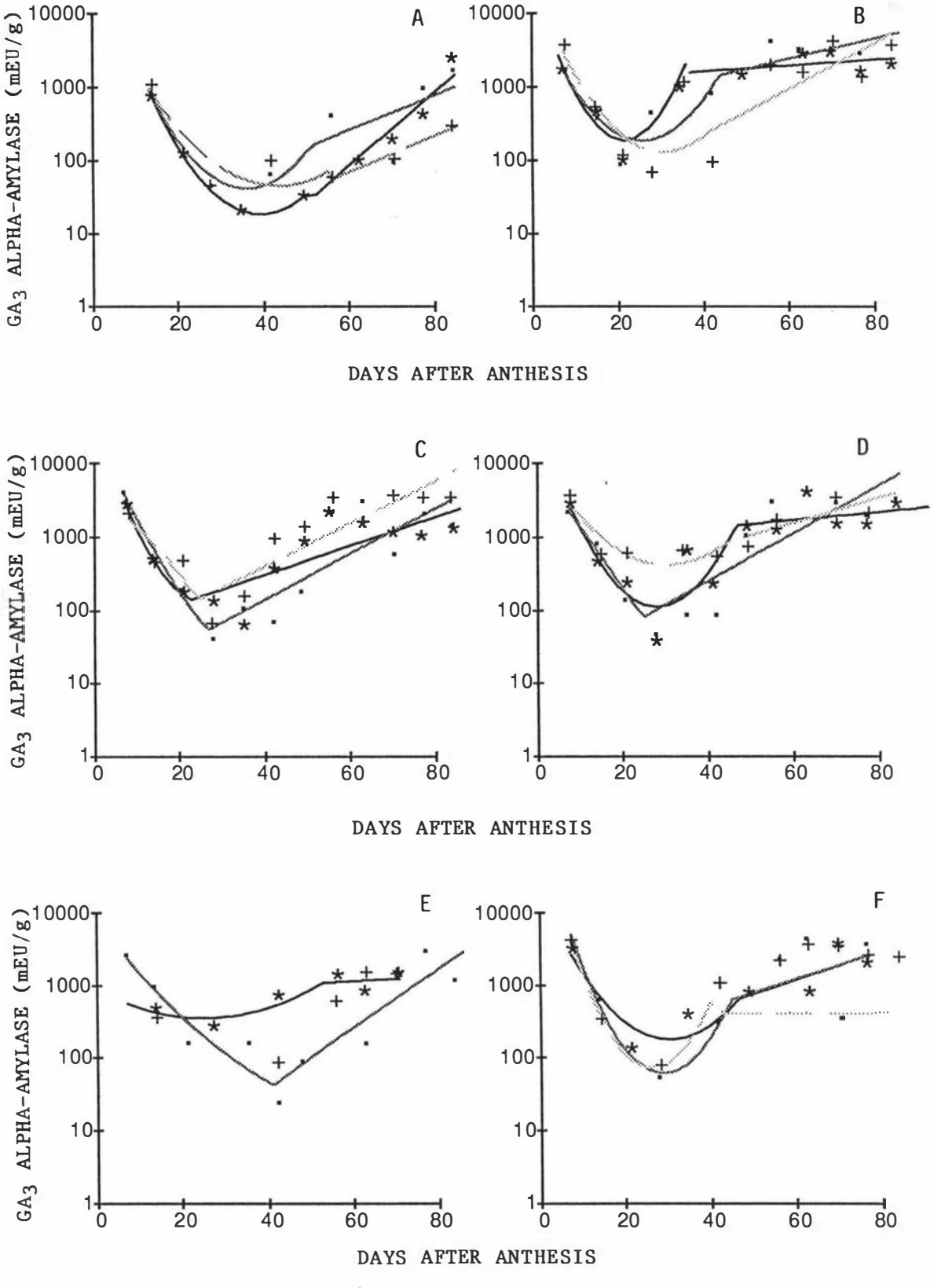

A
B
C
D
E
F
10000
1000
100
10
1
0
20
40
60
80
GA3 ALPHA-AMYLASE (mEU/g)
DAYS AFTER ANTHESIS

Figure A.42. Change in GA_3 a-amylase during grain development of the six generations of cross 3 wheat ripening in the cool environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

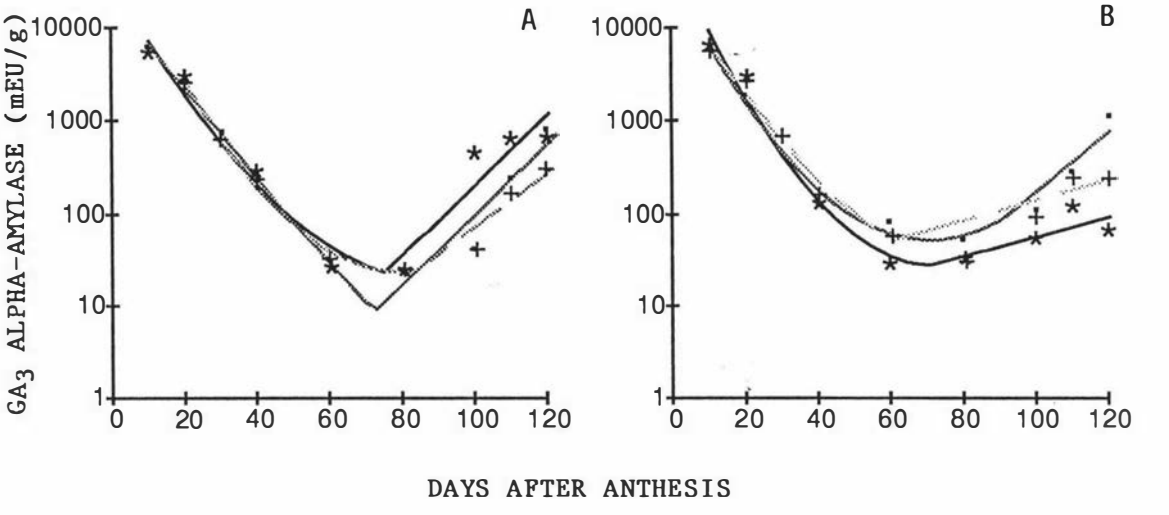
. observed values in block 2.

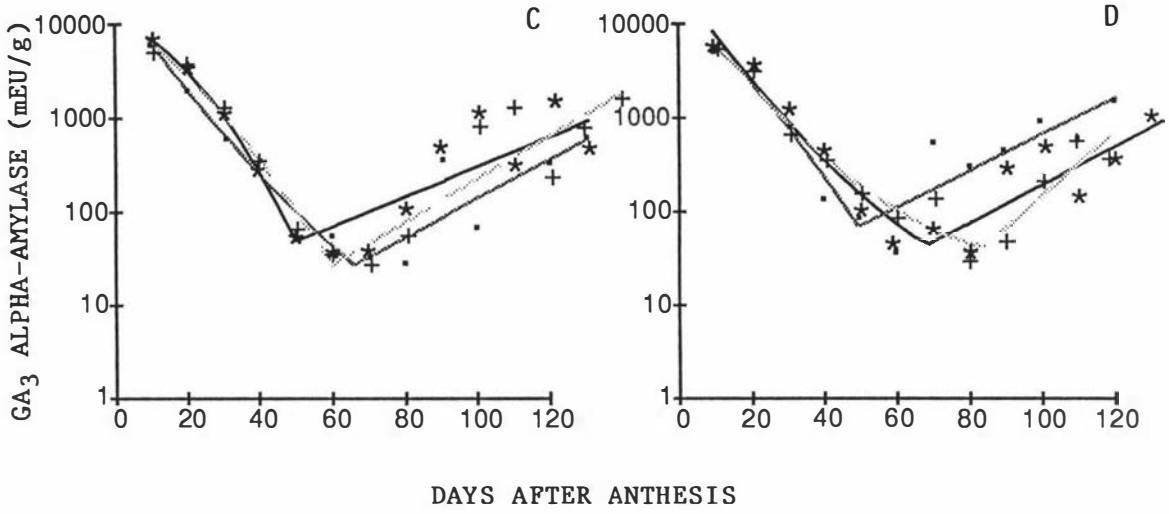
\+ observed values in block 3.

——— predicted values in block 1.

— — — predicted values in block 2.

.... predicted values in block 3.


A
B
10000
1000
100
10
1
0
20
40
60
80
100
120
GA3 ALPHA-AMYLASE (mEU/g)
DAYS AFTER ANTHESIS


C
D
10000
1000
100
10
1
0
20
40
60
80
100
120
GA3 ALPHA-AMYLASE (mEU/g)
DAYS AFTER ANTHESIS

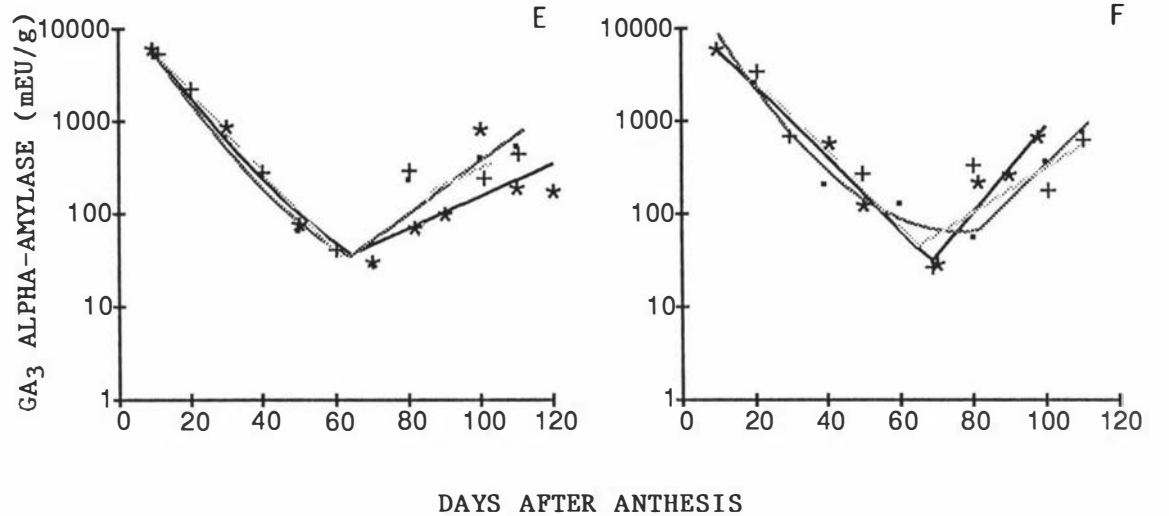

E
F
10000
1000
100
10
1
0
20
40
60
80
100
120
GA3 ALPHA-AMYLASE (mEU/g)
DAYS AFTER ANTHESIS

Figure A.43. Change in colour score during grain development of the six generations of cross 1 wheat ripening in the warm environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

— — — predicted values in block 2.

.... predicted values in block 3.

R^2 range from 88.50-100.00%

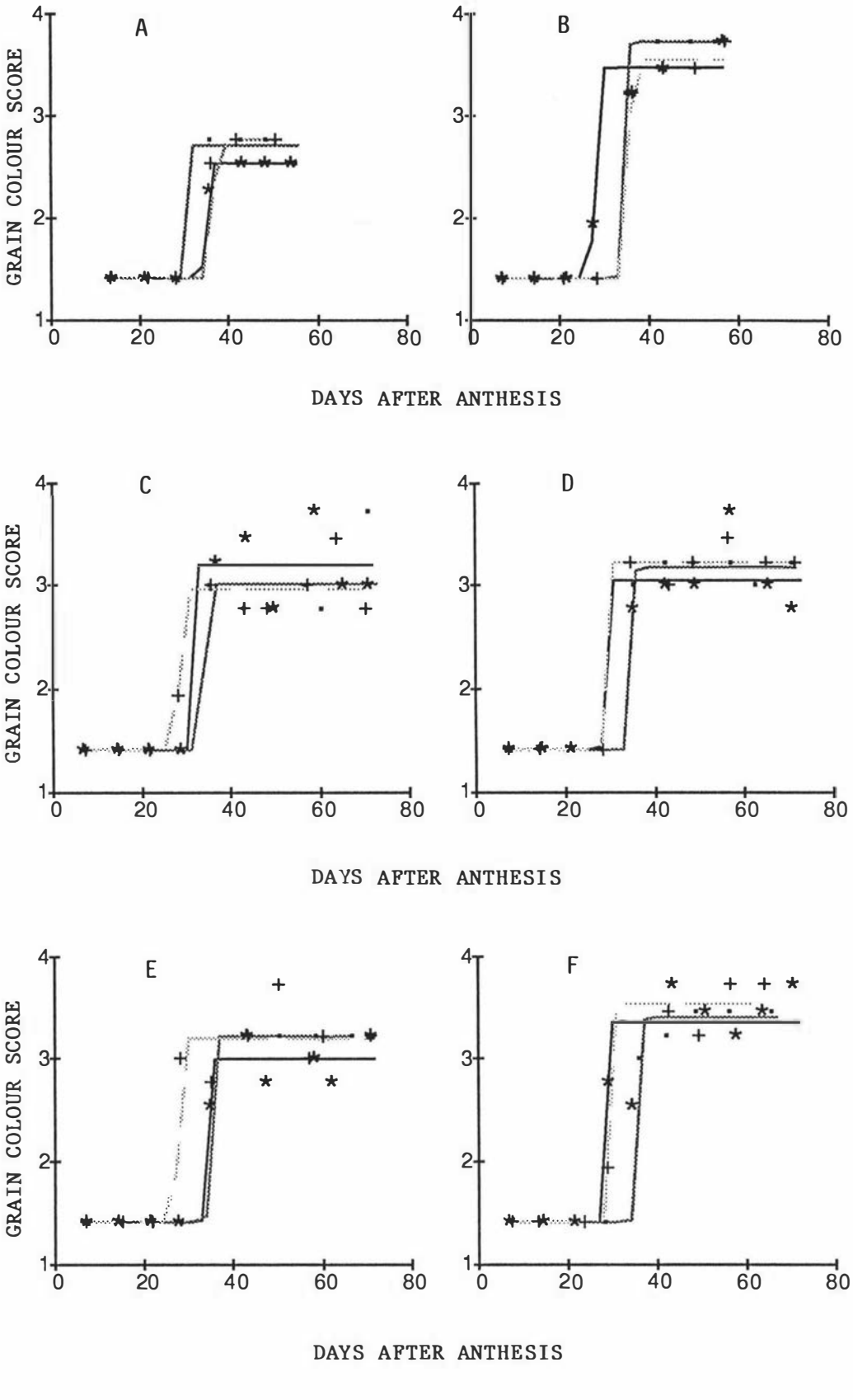

A
B
C
D
E
F
GRAIN COLOUR SCORE
DAYS AFTER ANTHESIS
1
2
3
4
0
20
40
60
80

Figure A.44. Change in colour score during grain development of the six generations of cross 1 wheat ripening in the cool environment.

A : Tordo

B : Karamu

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Karamu)S_1

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

_ _ _ _ _ predicted values in block 2.

.... predicted values in block 3.

R^2 range from 86.36-100.00%

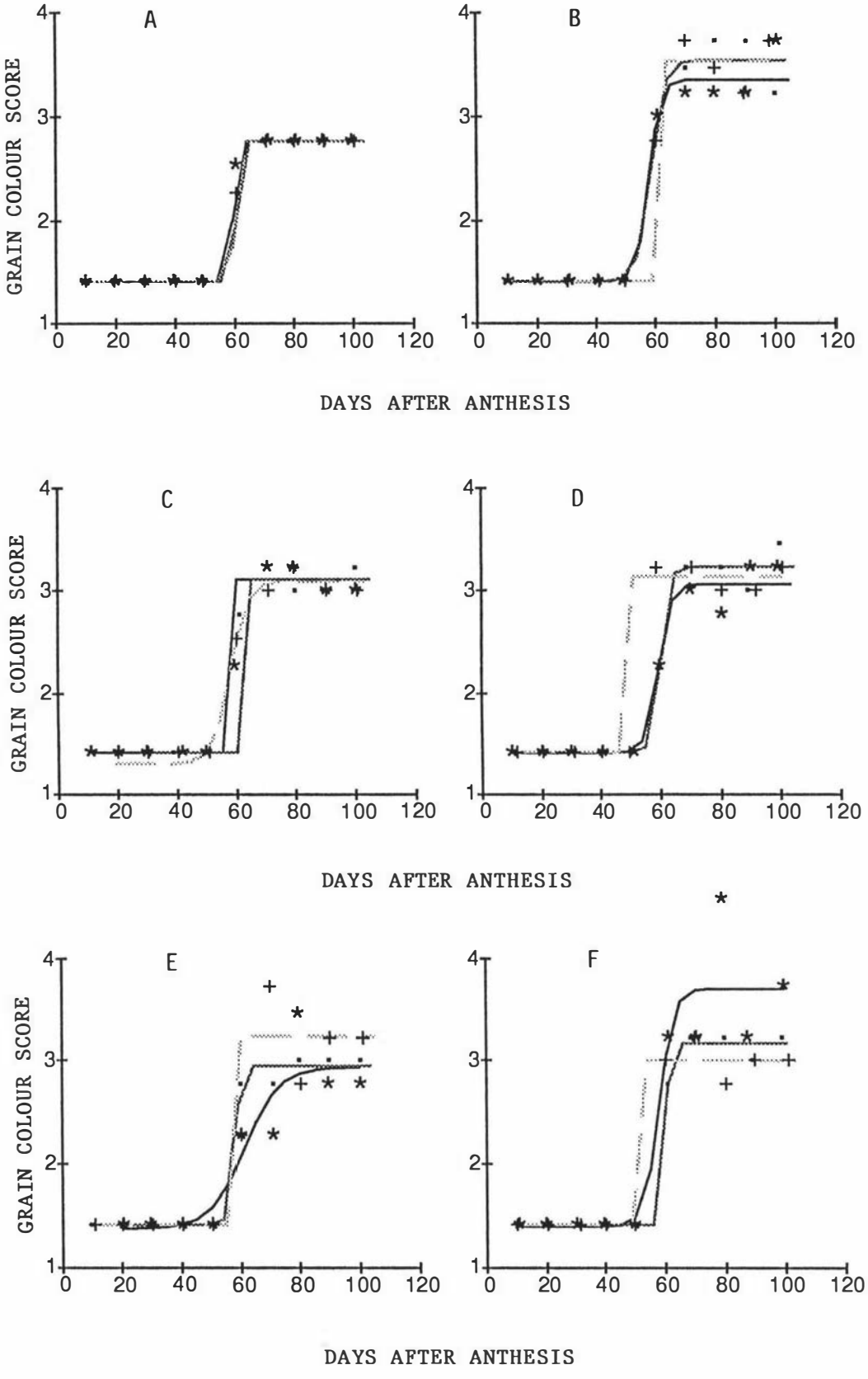

A
B
C
D
E
F
GRAIN COLOUR SCORE
DAYS AFTER ANTHESIS
1
2
3
4
0
20
40
60
80
100
120

Figure A.45. Change in colour score during grain development of the six generations of cross 2 wheat ripening in the warm environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : $BC_1(Tordo)S_1$

F : $BC_1(Gabo)S_1$

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

— — — predicted values in block 2.

.... predicted values in block 3.

R^2 range from 81.38-100.00%

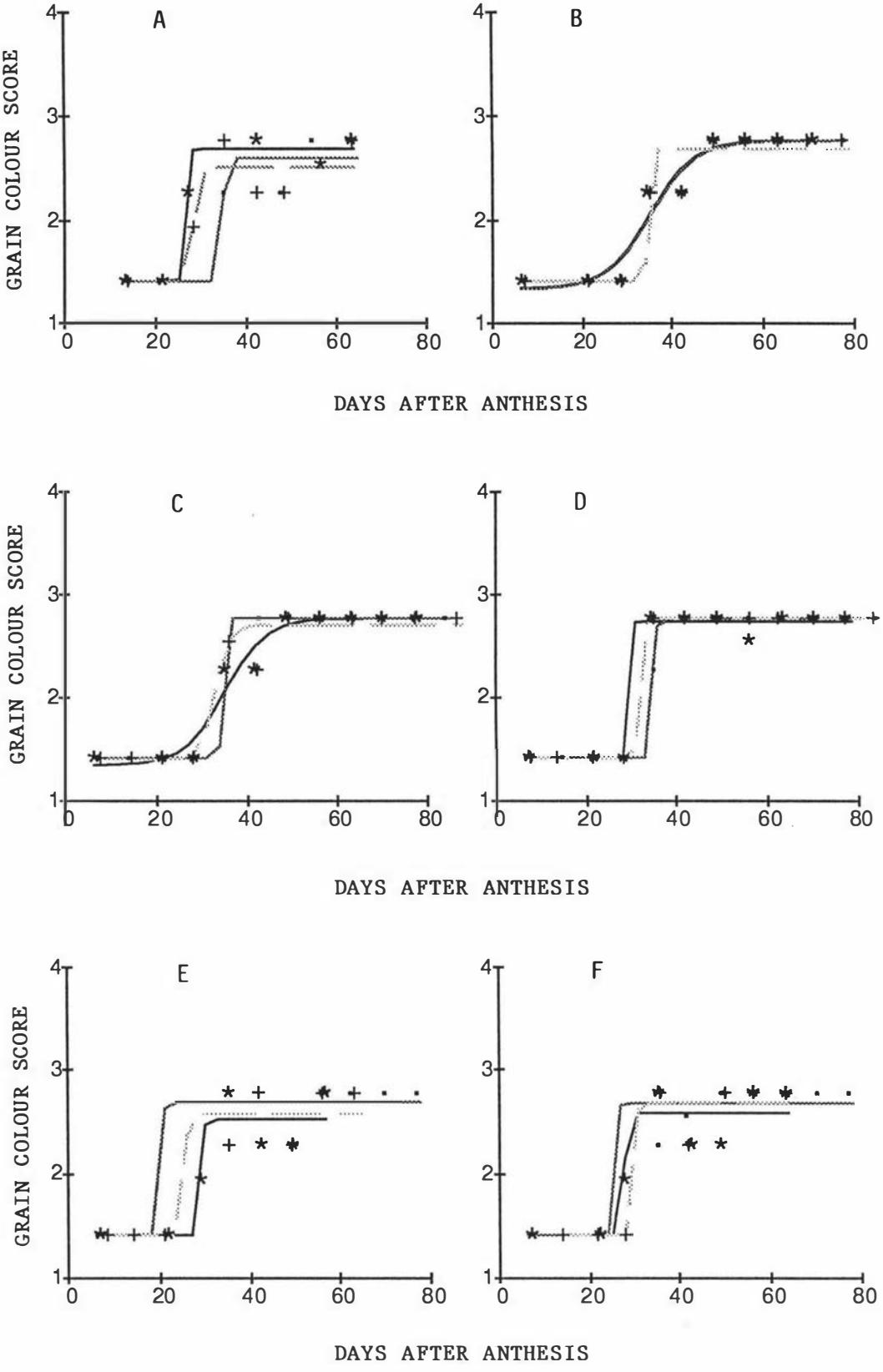

A
B
C
D
E
F
GRAIN COLOUR SCORE
DAYS AFTER ANTHESIS
1
2
3
4
0
20
40
60
80

Figure A.46. Change in colour score during grain development of the six generations of cross 2 wheat ripening in the cool environment.

A : Tordo

B : Gabo

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Gabo)S_1

* observed values in block 1.

. observed values in block 2.

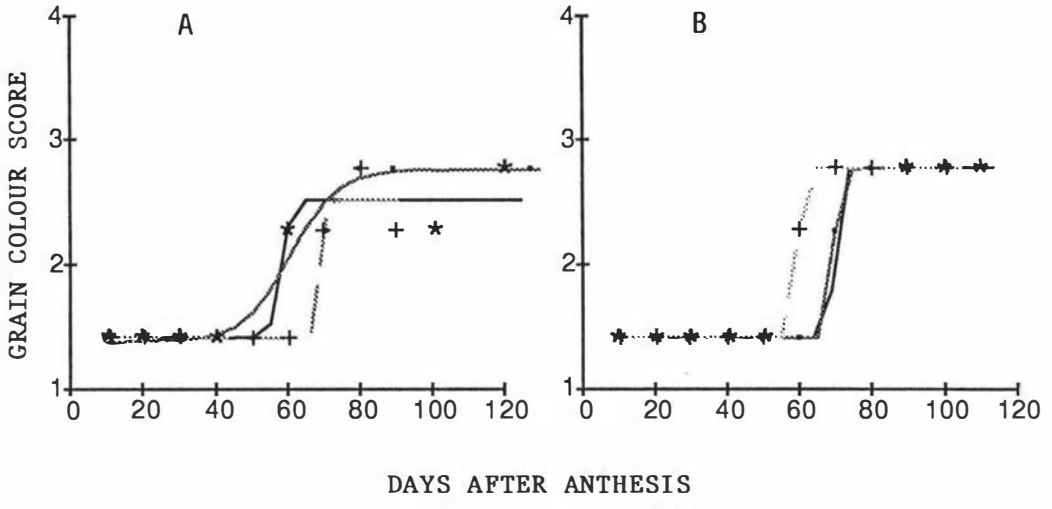
\+ observed values in block 3.

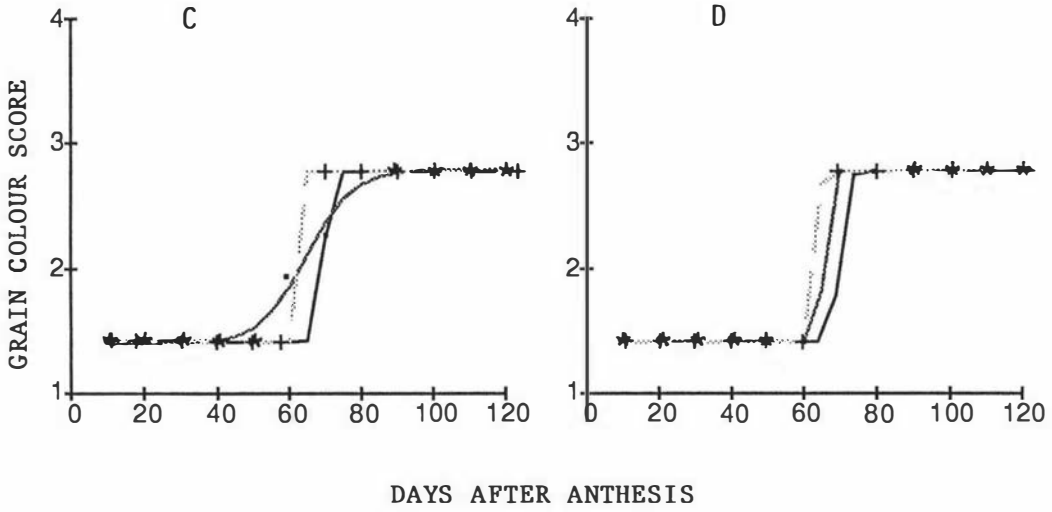
——— predicted values in block 1.

. ——— predicted values in block 2.

.... predicted values in block 3.

R^2 range from 93.37-100.00%


A
B
GRAIN COLOUR SCORE
1
2
3
4
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS


C
D
GRAIN COLOUR SCORE
1
2
3
4
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

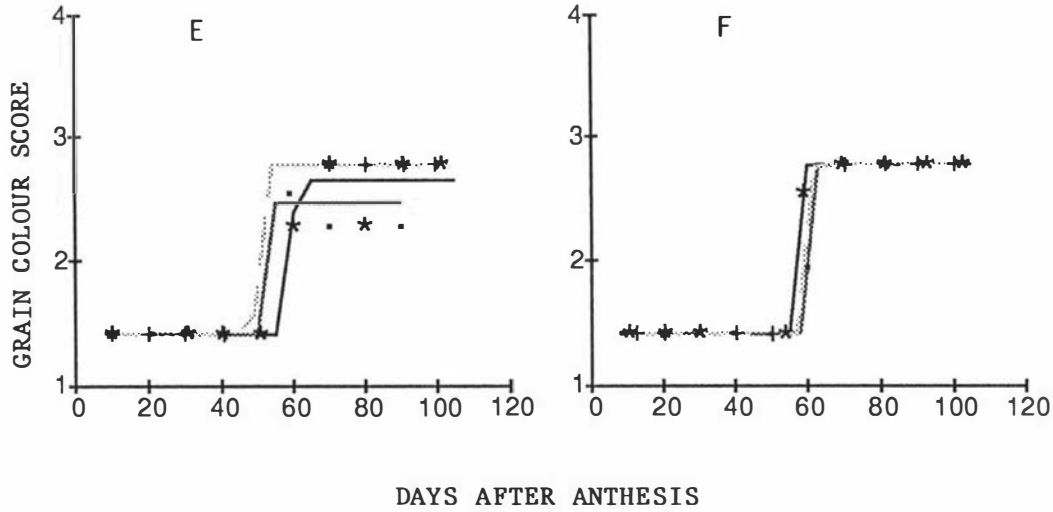

E
F
GRAIN COLOUR SCORE
1
2
3
4
0
20
40
60
80
100
120
DAYS AFTER ANTHESIS

Figure A.47. Change in colour score during grain development of the six generations of cross 3 wheat ripening in the warm environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : $BC_1(Tordo)S_1$

F : $BC_1(Sonora\ 64A)S_1$

* observed values in block 1.

. observed values in block 2.

\+ observed values in block 3.

——— predicted values in block 1.

——— predicted values in block 2.

.... predicted values in block 3.

R^2 range from 79.78-100.00%

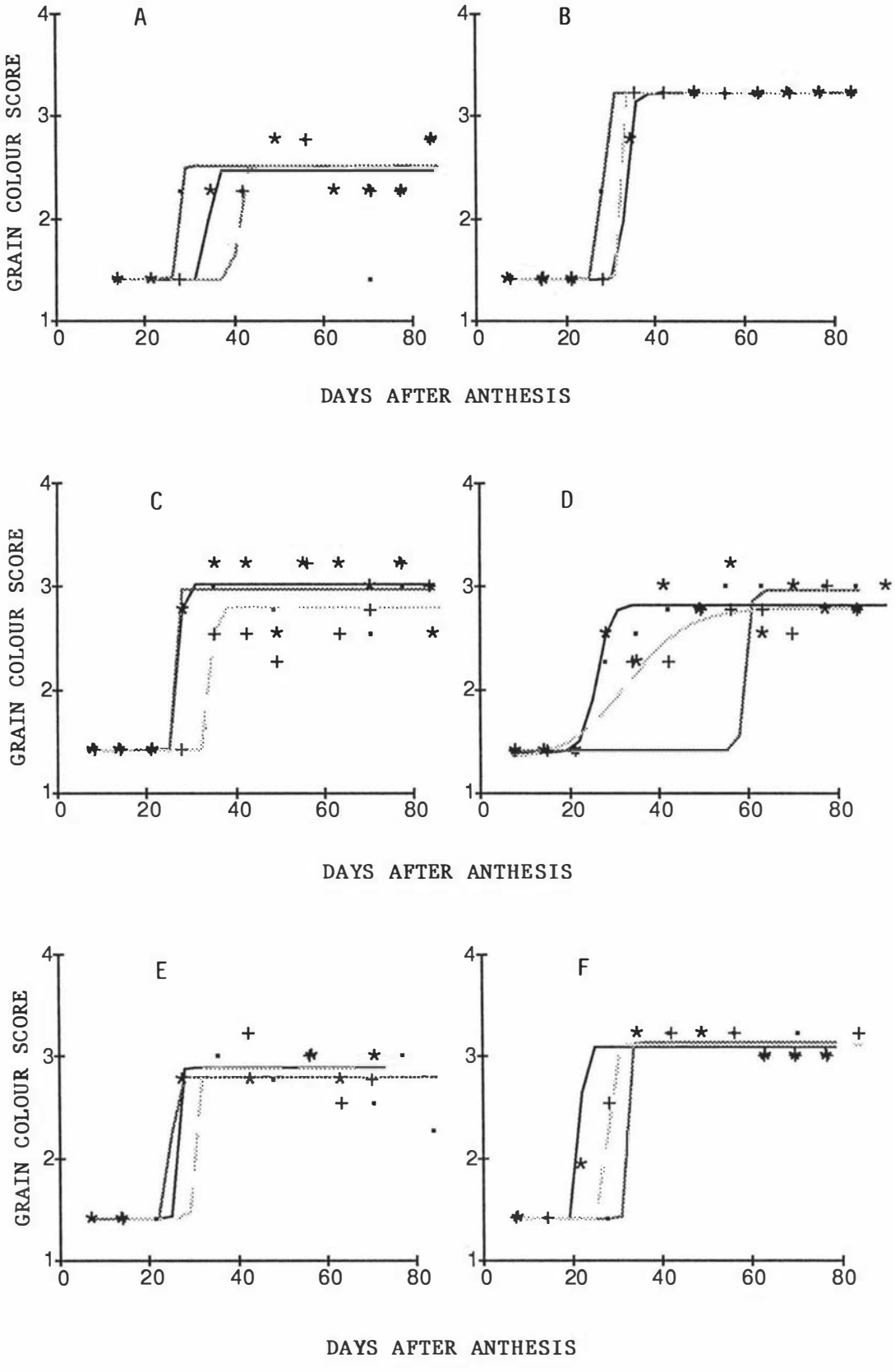

A
B
C
D
E
F
GRAIN COLOUR SCORE
DAYS AFTER ANTHESIS
1
2
3
4
0
20
40
60
80

Figure A.48. Change in colour score during grain development of the six generations of cross 3 wheat ripening in the cool environment.

A : Tordo

B : Sonora 64A

C : F_2

D : F_3

E : BC_1(Tordo)S_1

F : BC_1(Sonora 64A)S_1

* observed values in block 1.

. observed values in block 2.

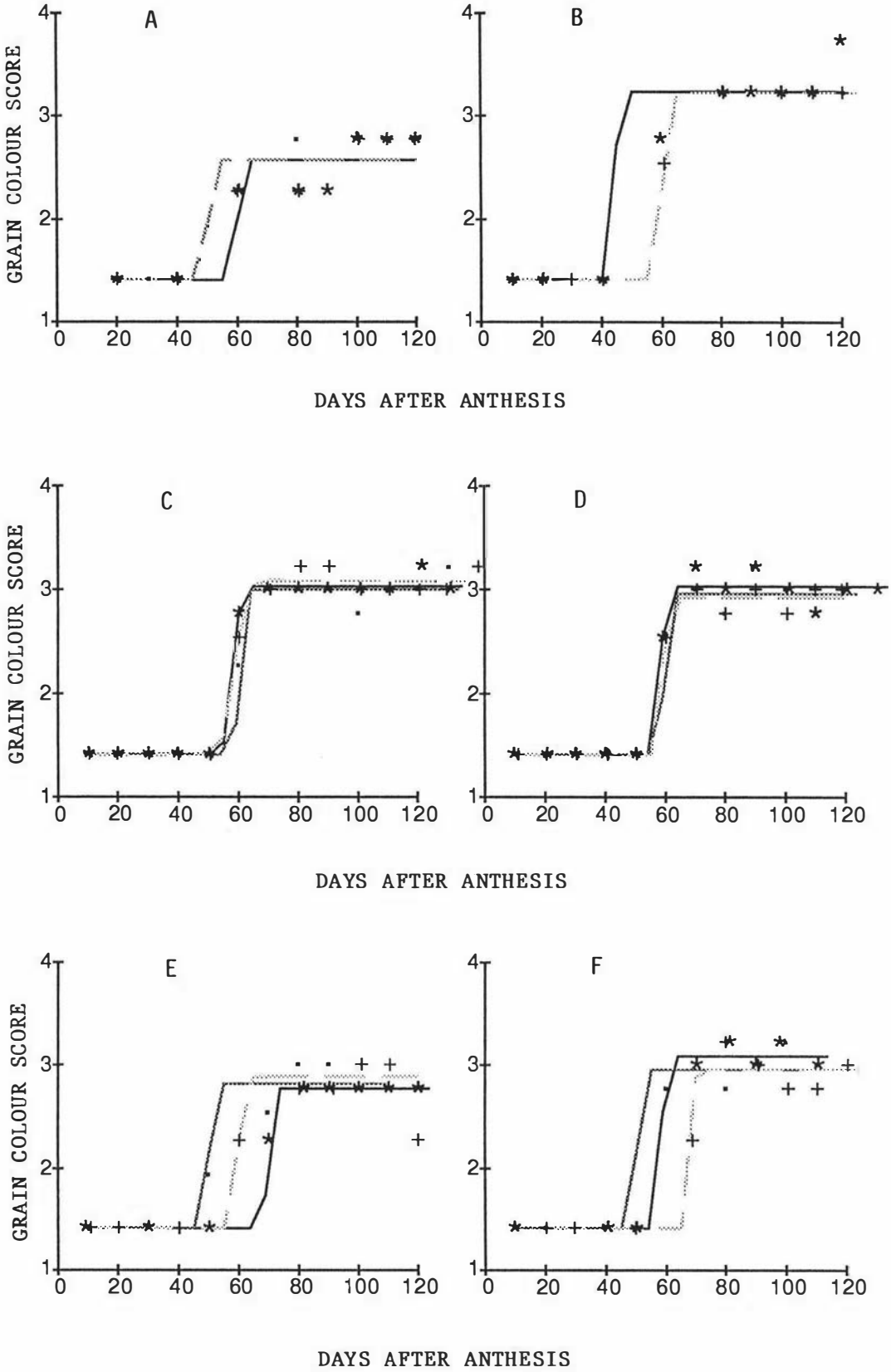
+ observed values in block 3.

——— predicted values in block 1.

— — — predicted values in block 2.

.... predicted values in block 3.

R^2 range from 86.51-100.00%


A
B
C
D
E
F
GRAIN COLOUR SCORE
DAYS AFTER ANTHESIS
1
2
3
4
0
20
40
60
80
100
120