GENOTYPIC AND ENVIRONMENTAL EFFECTS ON GROWTH HABIT IN WHEAT (*Triticum aestivum* L.)

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In the name of GOD the most compassionate and the most merciful.

In memory of my father and brother

ABSTRACT

A large part of wheat's world-wide adaptability is due to flexibility arising from spring-winter habit of growth. Genetic and environmental effects on growth habit in wheat were studied by considering the response patterns of 43 diverse lines to combined variations in temperature and photoperiod under natural conditions in the Manawatu region of New Zealand. Four environments were sampled by having a range of sowing dates from early winter to early summer.

The responses were evaluated using 14 developmental and adaptive attributes, and different techniques of univariate and multivariate analyses. Two pooled analyses were used; (a) 37 genotypes over all 4 environments (excluding six genotypes which did not flower in the two later sowings, (b) all 43 genotypes pooled over two early sowings. Estimates of heritability and genotypic correlation were obtained as well as the usual phenotypic analyses of ordinary correlation and genotype X environment patterns.

There was highly significant genotypic variation for all characters except leaf appearance and tiller production rates. Macro environment variance was the largest significant variance component, indicating that all characters were affected in a major way by environmental effects. Genotype X environment interaction variance was non-significant only for the numbers of fertile tillers and total tillers (in both analyses), and for main stem height in analysis (a). The narrow sense full heritabilities estimated by analysis (a) were very low (0.06% - 3.7%) for flowering characters, leaf appearance and tiller production rates; low (11% -18.5%) for leaf, spikelet and internode numbers; and moderate (34% - 57%) for tiller fertility ratio, fertile and total tiller numbers, main stem height and peduncle length. However, the restricted heritabilities were moderate to high for most of the characters (except leaf appearance and tiller production rates). Because of the narrower range of environments, but broader range of genotypes, in analysis (b), genotypic variance and heritability estimates were higher than in analysis (a).

Genotypic correlation was highly significant between flowering characters and leaf number (0.81 - 0.998). It was also highly significant between these characters and total tiller number, and negative and highly significant between the flowering characters and fertility ratio of tillers. Genotypic correlation between spikelet number, and flowering characters and leaf number was significantly moderate to high.

Phenotypic correlation for only the flowering characters, leaf and spikelet numbers was in good agreement with genotypic correlation in analysis(a). Despite of highly significant and negative phenotypic correlation between leaf appearance as well as tiller production rates and the flowering characters, the genotypic correlation between them was low and non-significant. This was in moderate level for fertile tiller number, main stem height, peduncle length and internode number.

General performances (line means) and response patterns of genotypes to environments (GE means) were significantly different. Six genotypes did not flower in spring sowings and one genotype (CRAW 45) flowered very late only on a few tillers. They were therefore classified simply as 'true winter wheat'. Duration of growth cycle was dependent on pattern of response, and was generally indicated by a larger number of leaves. The number of spikelets increased also, in parallel to increase in leaf number.

Genotype x environment means of seven characters, which showed highly significant genotype x environment interaction, were subjected to principal component analysis in order to delineate the genotypes on the basis of similar response pattern. This resulted in two principal component scores for each genotype for each character. Then cluster analysis was applied successfully to classify the genotypes on the basis of these scores. Another five groups were recognised in this way, and defined according to their means of principal component score for each character. The five group were as follows.
(1) Facultative wheats with moderate vernalization response and photoperiod sensitivity; (2) semi-spring wheats with moderate vernalization response and day neutral (photoperiod insensitive), (3) spring wheats with weak vernalization response and day neutral; (4) spring wheats with strong photoperiod sensitivity and weak or no vernalization requirement, (5) spring wheats with relatively strong photoperiod sensitivity and no vernalization response.

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INTRODUCTION

1.1 Distribution and classification of wheat

Wheat is grown in a wide range of environments around the world, in almost every country from within the Artic Circle to the equator (Figure 1.1). Wheat production is presently concentrated between 30° to 60° North and 27° to 40° South latitudes (Briggle and Courtis 1987). It is expected that the wheat area will be expanded into even colder, higher, wetter, drier and hotter regions (FAO 1983).

Wheat has been able to become the most important and the most widespread crop in the world because of its great adaptability to various environments. This adaptability is substantially due to the plant growth habit (spring vs. winter) and photoperiod sensitivity which constitute variation in the timing of wheat development (Gotoh 1979 Hoogendorn 1984). Illustration of this is that the wheat crop is sown and harvested within a period of 80 days in Canada but within almost a full year in northern Europe (Hoogendorn 1984).

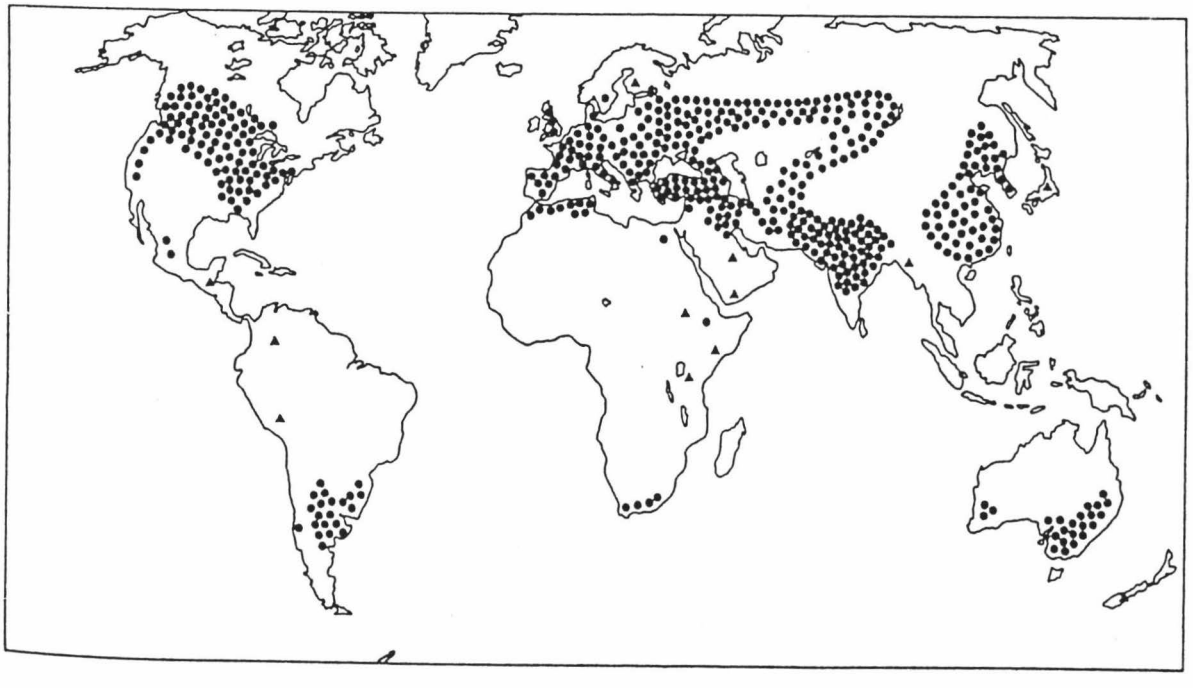


Figure 1.1 Wheat area and its distribution in the world in 1982, (FAO, 1983).

● - 500000 ha, ▲ - 50000 < regions < 500000 ha.

Wheat has been classified by growth habit into three types (CIMMYT 1987) as follows:

I). Winter wheats: have absolute vernalization requirement and are planted in autumn. They cannot develop without a continuous cold period of temperature (0-11 °C) of usually 40 days.

II). Spring wheats: have little or no vernalization requirement. They have a short growth cycle and may not survive in an extended period of freezing temperature. Therefore, they are usually planted in spring.

III). Facultative wheats; have attributes of both, are intermediate between spring and winter types and have moderate vernalization requirement. They have adaptations to fit fairly specific niches (Table 1.1).

1.2 Breeding for matching genotypes with enviroments

Crop production in the world is limited largely by biotic and abiotic environmental stresses such as pest and diseases, drought, cold and heat. On the one hand, the amelioration of environments to avoid these may not be economically and technically feasible. On the other hand, genetic improvement of crop adaptation and resistance is an economical, practical and viable solution (Blum 1988). For this reason, one of the important goals of wheat breeding is the development of wheat cultivars adapted to specific climatic conditions.

Of the basic physiological processes controlling plant adaptation, phenology and phasic development are strongly related to stability in yield performance over various environments (Blum 1988). Plant phenology in the winter cereals is controlled largely by sensitivity to photoperiod and vernalization requirements (Blum 1988). Vernalization is a cold treatment that induces, or at least promotes, flowering (Napp-zinn 1987).

Table 1.1 Distribution of different types of wheat in the world (CIMMYT 1986).
(% of total wheat area)

Region	SW	WW	FW
World	56	29	7
Developing Countries	67	13	10
Developed Countries	41	53	0
Estern Europe and USSR	7	93	0
Western Europe (e.g. Franc)	1	94	0
USA	21	75	0
Iran	29	21	50
Australia	100	0	0

SW = Spring wheat
WW = Winter wheat
FW = Facultative wheat

The differences in vernalization requirement between genotypes is governed by a system of genes (Vrn/vrn) which consequently control the growth habit. Three to five genes (vrn1, vrn2,...,vrn5) have been reported for controlling vernalization response (Pugsely 1971,1972; Mayestrenko 1974; Halloran 1976: Stelmakh 1987). There is also a continuous variation in vernalization requirement from spring to winter habit indicating polygenic control of vernalization response (Snape *et al.* 1976; Flood and Halloran, 1986).

Photoperiod sensitivity, by definition, is a response to change in the length of day. Generally the photoperiod sensitive genotypes are delayed in heading by short days, while insensitive genotypes head in a normal time regardless of photoperiod (Welsh *et al* 1973; Lupton 1987). Response to photoperiod in wheat is controled by two to three major genes where sensitivity is recessive (ppd) and insensitivity is dominant (Ppd), (Mcintosh, 1973; Welsh *et al.* 1973).

Vernalization and photoperiod response are often used by breeders to adjust the life cycle of the wheat crop to suit environmental conditions. Both of these responses are also used in wheat modeling and yield simulation of various winter or spring types of wheat (Hoogendorn, 1984; Blum, 1988).

The matching of crop development to the pattern of soil water availability is also considered importatnt for improving yield under drought conditions. Since a short duration of growth is an important attribute of drought escape, earliness forms a part of most breeding programms designed to produce cultivars adapted for drought conditions (Bidinger and Wictombe, 1989).

1.3 Genotype and Environment controlling wheat development

Wheat development can be divided into three distinct phases:
vegetative phase (from sowing to ear initiation), reproductive phase (from ear initiation to anthesis) and grain development phase (from anthesis to ripening) (Evans, 1975; Kirby and Appleyard, 1984; Simmons, 1987). The timing of these phases depends on the environment and genotype. Main environmental factors which influence plant development are temperature and daylength. The

crop husbandry decision which governs this outcome is sowing date (Hoogendorn 1984).

Generaly, development towards flowering is faster the higher the temperature and the longer the day. But, in the case of genotypes with vernalization requirement genes (vrn), exposure to low temperature in early growth is also essential for flowering. In total therefore, the timing of development phases is influenced by growth habit potential. Also, yield components such as number of leaves, spikes, spikelets and florets are strongly dependent on the interaction of environmental factors (mainly temperature and daylength) and genotypic properties (i.e. the Vrn/vrn and Ppd/ppd genes and other genes). The flow chart in Figure 1.2 illustrates the effects of genetic and environmental factors on wheat development.

In most growth habit studies, a few genotypes only have been examined. However, Ford *et al*, 1981, Davidson *et al*, (1985) and Hoogendorn (1984) examined a large number of genotypes, but they considered only a few characters in separate analyses and did not consider many relevant characters. Also they did not study the association amongst the characters.

In the study presented here, the effects of environment and genotype on growth habit and the timing of development in wheat have been examined by using a large number genotypes (43) and considering a wide range of relevant characters. Also, genotypic statistics for this wide germplasm (such as genotypic and phenotypic variances, heritablity, genotypic and phenotypic correlations) were obtained. Two multivariate techniques (principal component analysis and cluster analysis) have been used successively to classify the genotypes in relation to their requirement for vernalization and sensitivity to photoperiod. The results are discussed with respect to both wheat physiology and breeding.

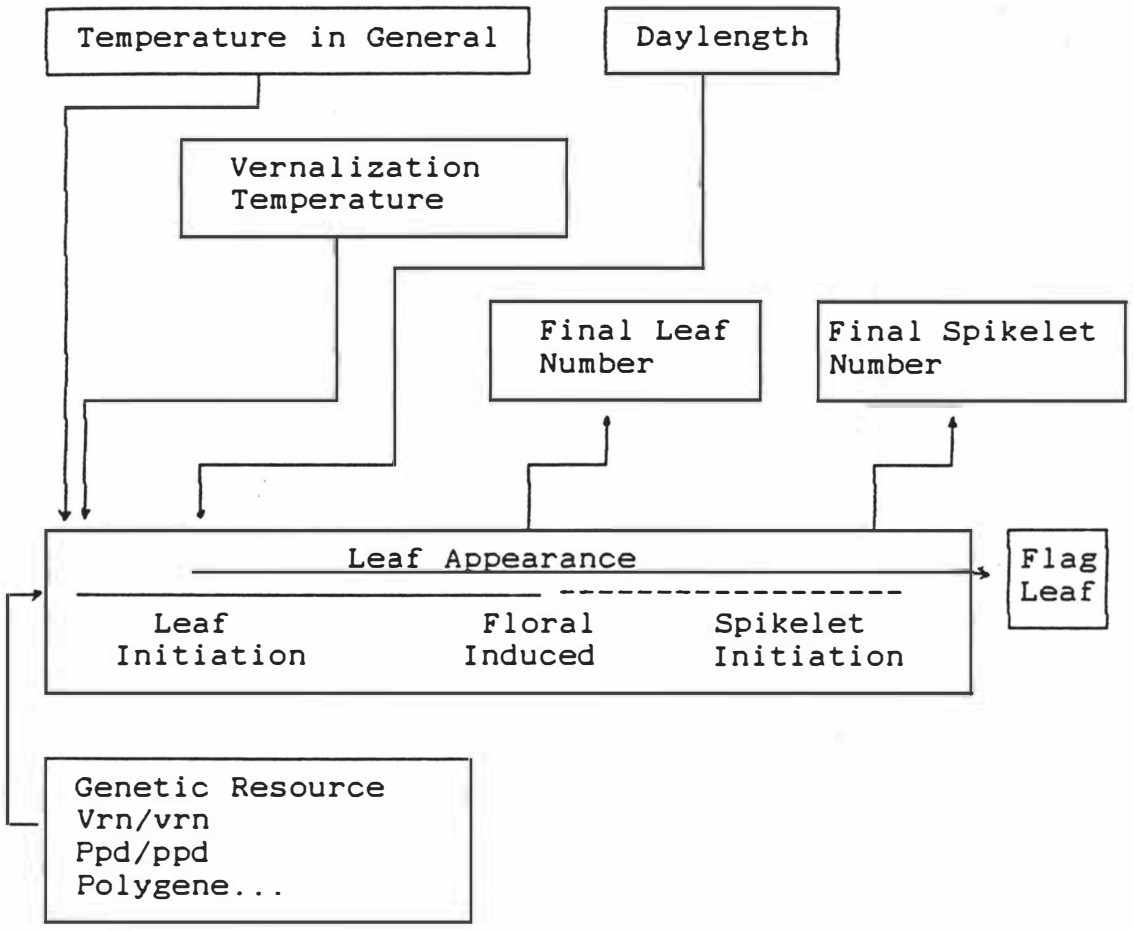


Figure 1.2 Genetic and environmental effects on development phases of wheat and consequently winter-spring habit of growth in wheat.

Chapter 2

REVIEW OF LITERATURE

2.1 Wheat Development and its Growth Cycle

The life cycle of wheat can be divided into a series of phases from germination until harvesting. A number of distinct stages can be recognised during these phases (Figure 2.1). Development is an increase in complexity of form, and is measured as the time taken to reach defined stages (Kirby and Appleyard 1984).

The main factors which influence development are temperature, day-length and culivar (Kirby and Appleyard 1984). Evans *et al.* (1975) reported that rate of development is also affected by radiation intensity and availability of water and nutrition, while cultivar effect is less important.

The series of developmental processes which are common to all environments and genotypes are described in the following sections.

2.1.1 Germination and Emergence

Within the mature wheat grain the coleoptile covers the shoot apex which has already initiated three or four leaf primordia (Kirby and Appleyard 1987). Once the embryo is fully imbibed with water, leaf initiation and tiller development start, and proceed without interruption as the seed emerge from the

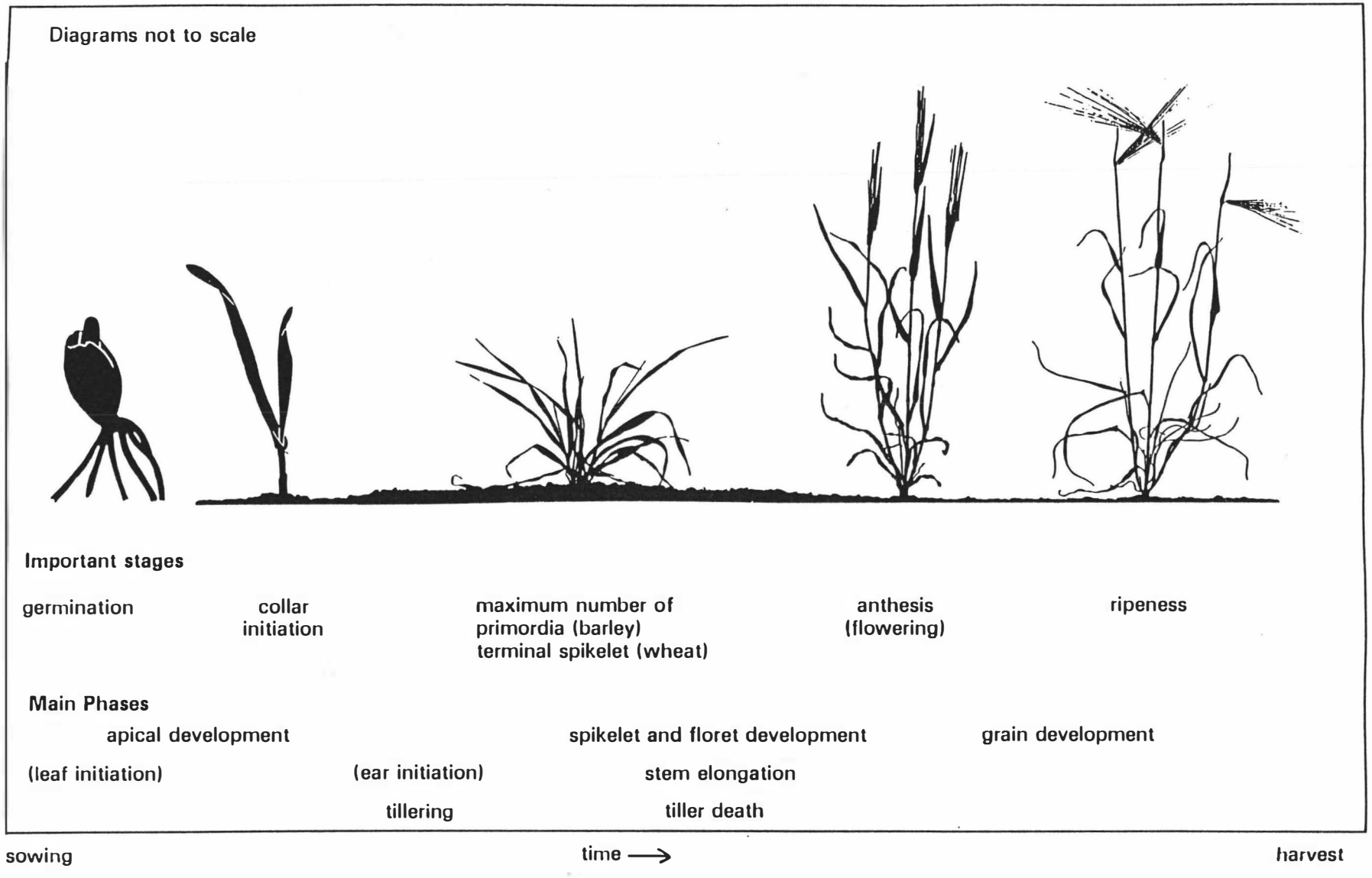


Figure 2.1 Developmental phases during life cycle of wheat (Kirby and Appleyard, 1984).

soil (Kirby and Appleyard 1987; Hay and Kirby 1991). Germination occurs between 4° and 37 °C, with 20-25 °C optimal. The minimum water content for germination is 35-45% of grain dry weight. Light is not of great importance in controlling germination of wheat (Evans *et al.* 1975).

Some varieties have a degree of seed dormancy which prevents germination for a while after harvesting. The degree of dormancy depends on the temperature at which the seeds are germinated. A low temperature (15 °C) is effective for breaking dormancy (Ready *et al.* 1985). Strend (1989) and Sereeprasert (1990) also reported that higher temperature and more intense radiation during the grain maturation period generally reduced seed dormancy.

The coleoptile grows and penetrates to the surface and seminal roots extend into the soil. When the coleoptile is at or just above the surface, extension stops due to the response to the light . The coleoptile may grow up to 20 to 100 mm, depending upon sowing depth and genotype (Kirby and Appleyard 1987).

The time to emergence varies with the sowing date mainly due to temperature differences, although,soil water status is also important. Increasing the depth of sowing, also increases the time for seedling emergence (Ashraf and Abushakra, 1978). Over a range of temperature from 0° to 30 °C the response of seedling emergence to temperature is approximately linear (Kirby and Appleyard 1987). Because of the linear nature of the response, it is possible to use thermal time (accumulated temperature; Weir *et al.* 1984) to analyze and predict seedling emergence. On this basis, the number of degree-days which is needed to emergence varies from about 70 to 200 .

The rate of emergence shows genetic variation in wheat and is positively correlated with coleoptile length and plant height (Allan *et al.* 1962, Evans et al. 1975). The growth from germination until the emergence of the first green leaf

is dependent on reserve carbohydrates in the endosperm (Williams, 1960). According to Schlehuber and Tuker (1967), seed protein content may be the main factor influencing seedling development.

2.1.2 Root Growth

Two distinct root systems develop in wheat, the seminal roots arising directly from or below the seed, and the adventitious roots that arise from the nodes of the stem above the seed (Passioura, 1972; Evans et al. 1975; Kirby and Appleyard 1984).

Root growth may exceed shoot growth at low temperatures, but as temperature rises the growth of shoots increases more than that of roots (Bruower, 1966). Thus, shoot growth appears to have a higher optimum temperature than root growth.

Each tiller normally develops its own system of adventitious roots and each root system normally supplies the shoot to which it belongs (Boatwright and Ferguson, 1967; Kirby and Appleyard 1984).

Winter cereals tend to produce a larger weight of roots than spring sown ones, presumably due to the longer period of growth at low temperatures (Evans et al. 1975). Genetic variation has been reported in the rooting pattern, distribution and size of root in wheat (Derera *et el.* 1969; Evans and Bhatt, 1977; O'Brien, 1978; Blum, 1988). However, screening and selection for such differences is difficult to achieve, particularly in the field.

Shoot growth is dependent on root function and the role of roots is not only for nutrient and water uptake. Roots may also synthesize amino acids, and act as a source of growth substances such as cytokinins for the shoots, but the

significance of their role in this respect is not clear (Evans et al. 1975).

2.1.3 Development of Shoot Apex

The shoot apex is formed in the embryo during grain growth and is well established in the mature seed. It is made up of a smoothly meristemic dome on the flanks of which are formed the leaf and spikelet primordia (Kirby and Appleyard 1984). The dome grows by cell division until it reaches a critical size when there is a change in the orientation of the plane of the division of cells in the dermatogen or corpus layers. This initiates a bulge or ridge of tissue, a primordial organ which grows into a leaf or spikelet (Barnard, 1964; Kirby and Appleyard 1987). During the first part of life cycle which the wheat plant is a seedling the dome initiates leaf primordia; later it initiates spikelet primordia.

The transition from vegetative to reproductive development which is a pivotal event in the life cycle of the main shoot, occurs when the collar, the first floral primordium, is initiated (Delecolle et al. 1989; Hay and Walker, 1989). The number of leaves produced is a consequence of when the transition occurs (Kirby and Appleyard 1984, 1987; Hay and Kirby 1991). There are no external signs or obvious morphological change at the apex to indicate this transition. In other words, vegetative and early floral stages are similar and differences only become distinguishable as the spikelets develop (Kirby and Appleyard 1987 Hay and Kirby, 1991).

The stage at which differentiation of the primordia into a spikelet is first visible in the apex, is called double ridge stage. The plant at this stage will generally have between 4 to 10 leaves emerged on the main shoot depending on date of sowing and genotype (Kirby and Appleyard 1984). In spring wheat there is an immediate increase in the rate of initiation of primordia, each of which develop into a single spikelet (Kirby, 1974). However, under certain conditions,

winter wheat apices can continue to produce a few spikelet at the lower rate (leaf primordial) before the increase in rate occurs (Delecolle et al. 1989). The rate of initiation of spikelets has been shown to vary with temperature and daylength (Rawson, 1971; Rahman and Willson, 1977; Stern and Kirby, 1979; Kirby et al. 1987; Delecolle, 1989) as well as location, cultivar, sowing date and plant population density (Hay and Walker, 1989).

At the same time as the initiation of spikelets proceeds, each spikelet primordiom will initiate 8 to 10 floret primordia (Kirby and Appleyard 1984). Under the influence of genotype and environment the initiation of spikelet ceases when the last few primordia do not develop into spikelets, but become the glumes and florets of last spikelet which is known as terminal spikelet (Kirby and Appleyard 1984; Kirby and Appleyard 1987; Hay and Kirby, 1991). The apex at this stage is about 4mm long. The duration of this phase (from beginning of leaf initiation to terminal spikelet) varies from 50 days in spring wheats to 200 days in winter wheats (Kirby and Appleyard 1984; Kirby and Appleyard 1987), and the numbers of initiated leaves and spikelets during this period depend on variety and time of sowing.

Development of the apex is an importance factor in winter hardiness. Spring wheat sown in early autumn may develop rapidly in relatively high temperatures and long days. They may have an advanced floral apex before the onset of winter, and also be more susceptible to frost damage. After double ridges, when stem elongation begins, apices became vulnerable (George, 1982; Kirby and Appleyard 1987).

2.1.4 Development of Leaf

Leaf development and final morphology depends on genotype, onto-genetic position and environment. Leaf size, shape, cell size, stomatal distribution and

photosynthetic capacity are all sensitive to the environment (Jones, 1985). Growth of the photosynthetic leaf canopy also depends upon the rate of leaf production by the main stem and tillers, and upon the size of leaves.

The first leaf tip appears shortly after the coleoptile emerges from the ground, by which time about five leaves have been initiated by the apex of the main shoot (Baker et al. 1980; Hay and Kirby, 1991).

2.1.4.1 Leaf Appearance

Studies on graminaceous crops have shown that leaf appearance is related to temperature but since the stem apex and leaf extension zone are near to the soil surface, the controlling factor is the temperature of the surface layers of soil (Hay and Tunnicliffe wilson 1982). In practice , good linear relationships have been established between cereal main stem leaf number and accumulated air temperature (thermal time) above a base temperature which is estimated by regression methods (Baker et al. 1980). The base temperature for leaf emergence is about 0 °C (Baker 1986; Kirby and Appleyard 1987; Masle 1990). Kirby et al. (1982) suggested that base temperature for cereal leaf appearance can vary with sowing date.

While Friend, Helson and Fisher (1962) reported that photoperiod affects the rate of leaf appearance, it does not explain observed differences in field observations, and it has been suggested that leaf appearance rate is related to the rate of change of daylength (Baker et al. 1980).

The rate of leaf appearance is sometimes expressed in terms of 'phyllochron'. This is the period, expressed in thermal time, from the emergence of one leaf to the next and is the reciprocal of the appearance rate.

For example if rate of leaf appearance is 0.01 leaves /°C/day the phyllochron is 100 °C day (Kirby and Appleyard 1987; Cao 1990).

Leaves appear more or less regularly at an interval (phyllochron) of approximately 100 degree days. The observed range is 70-160 degree days, according to cultivar, sowing date and latitude (Baker et al. 1980; kirby et al. 1985). In some winter wheat crops the rate of leaf appearance may change in autumn or spring (Hay and Delecolle 1989). Other factors such as nitrogen level and water supply do not appear to affect the rate of leaf appearance (Kirby and Appleyard 1987)

2.1.4.2 Leaf Number

Generally, the number of emerged leaves provides an index of plant development (Kirby and Appleyard 1984, 1987;). The final number of leaf produced per shoot is clearly influenced by the timing of the switch from vegetative to reproductive development (Kirby and Appleyard 1984; Kirby 1990; Hay and Kirby 1991). The number of leaves produced on the main stem generally varies from even 7 to 14 leaves. Time to flowering is therefore affected strongly by the number of emerged leaves (Levy and Peterson 1974; Kirby and Appleyard 1984, 1987; Kirby 1990; Hay and Kirby 1991).

Vernalization and Long days reduce the number of leaves per stem (Halse and Weir 1970; Ford et al 1981; Kirby et al. 1985; Hay and Kirby 1991). Winter wheat produce more leave in early autumn sowing than late autumn sowing, but spring sowing of winter wheat leads to formation of more leaves, because the temperature is not low enough to complete vernalization.

The numbers of leaves on the tillers is proportional to the number of main stem leaves, but fewer are formed. Typically, tiller 1 will have two leaves two

leaves fewer than the main stem and tiller 2 will have one less leaf than tiller 1 and so on. When a tiller has 4-5 leaves the number of leaves is not further reduced with ascending tiller position (Stern and Kirby 1979). This reduction in number of leaves synchronizes development of the main stem with that of ear bearing tillers (Kirby and Appleyard 1987; Hay and Kirby 1991).

2.1.4.3. Leaf Expansion and Size

Leaf position is an important factor for leaf size and there is genetically determined upper limit to the size of a leaf at any node and intermediate leaf position may have maximum size of leaf (Gallagher 1979; Kirby and Appleyard 1987 Hay and Walker 1989).The size of leaf is governed by ontogeny, and environmental factors such as temperature, water supply, irradiance and nitrogen fertilizer act to modify the ontogenetic drift in leaf size (Fitter and Hay 1987). In grasses and cereals, leaf expansions controlled by the surface layers of soil surranding leaf extension zone during vegetative development (Peacock 1975), or by air temperature during reproductive development when stem extension has carried the leaf extension zone above the soil surface (Gallagher *et al.* 1979).

Gallager (1979), Hay and Tunnicliffe Wilson 1982 reported that the relationship between leaf expansion and accumulated temperature in temperate cereals is linear over the normal temperate range (0-25 °C) with base temperature near 0 °C.

Increased rates of leaf expansion at higher temperatures are generally associated with shortening of the duration of leaf expansion, which is Conveniently defined as the time elapsing between the achievement of 5 and 95 per cent of final leaf area (Gallager 1979). On the other hands, larger leaves has been reported due to longer duration of leaf expansion at low and intermediate temperatures (Milthorpe and Moorby 1979).

2.1.5 Development of Tillers

The number of ears per plant is an important component of yield therefore the number and the final size of tillers, and the timing of tillering have critical effects on final grain yield. The number of tillers varies with genotype, density of sowing, nutrient levels, water supply and plant growth regulators (Kirby and Appleyard 1984; Kirby and Appleyard 1987; Hay and Walker 1989).

The first stage in the formation of a tiller is the growth of a ridge of meristemic tissue in the axil of the basal leaf. The buds develop in the axil of the coleoptile and each of the lower leaves of the plant. They do not form in the axils of leaves which will subtend elongated internodes. The secondary tiller buds are formed on the primary tillers in the same way. In well watered condition with low density of sowing these may produce tertiary tillers (Kirby and Appleyard 1984; Hay and Kirby 1991).

In winter wheat the sequence is similar to spring wheat, but as there are more leaves produced on the main stem, there may be as many as 10 primary tiller buds produced, with a few secondary and no tertiary (e.g in European winter wheat, Kirby and Appleyard 1984; Kirby and Appleyard 1987; Hay and Kirby 1991).

The first tiller generally appears when leaf 3 of the main shoot is fully emerged and leaf 4 is emerging. Three phyllochrons after the appearance of the first leaf, subsequent primary tillers emerge at regular intervals of one phyllochron (Baker and Gallagher 1983; Kirby and Appleyard 1984; Kirby *et al.*

al. 1985; Masle 1985). The coleoptile tiller occur only some crops usually under the most favorable conditions (Peterson et al. 1982), but when it occurs, it is the first, coinciding with the appearance of the third main shoot leaf (Baker and Gallaghery 1983a).

Tillers do not become independent of their parent shoots until they have developed about three mature leaves, when adventitious roots may format their base (Evans *et al.* 1975). According to Friend (1966), the rate of tillerring is maximal at 25 °C, but Rawson (1971) suggested that greater number of tillers at lower temperatures, the slower rate being more than compensated for the greater duration of tillering.

Tillering stops in wheat when the main shoot is at the double ridge stage (Kirby and Appleyard 1984, 1987). Around the time that the main shoot apex reaches the terminal spikelet stage (Thorne and Wood 1988) or a short time after terminal spikelet stage (Kirby and Appleyard 1987) the tillers begin to die in the reverse order of their emergence. Often tillers that have formed more than 3 leaves at the terminal spikelet stage do not die, and this may be a critical size, related to dependence of the tiller on its parent shoot (Masle-Maynard and Sebillotte 1981; Kirby and Appleyard 1987). In a crop sown to a normal population density, the main shoots and tillers which ultimately bear synchronously maturing ears emerge over a period of up to 500 degree days (5 phyllochron , equivalent to 50 days at a mean temperature of 10 °C, Hay and Kirby 1991).

2.1.6 Stem Growth

The shoot apex in an autumn sown winter wheat, remain just below the surface until spring. Rapid stem elongation then Occurs and carries up the ear. Usually the mature stem comprises from five to seven elongated internodes,

(Internodes longer than 10 mm). Variety, plant population and other factors may affect this number (Kirby and Appleyard 1987). The unelongated internodes represent only a few millimeters at the base of the mature stem . Length of individual internodes increases from the lowest internodes to the peduncle (Kirby *et al.* 1985).

The stem extend rapidly after terminal spikelet stage and attaining its final length at anthesis. There is also a rapid dry matter increase during this period and the stem is the most rapidly growing part of shoot. Growth rates differ between genotypes and Rht dwarfing genes derived from Norin 10 appear to be one source of this variation (Brooking and Kirby 1981).

Leaf and internode growth are correlated, internode growth starts when the sheath of the subtending leaf is growing most rapidly (Kirby and appleyard 1984: Kirby and Appleyard 1987).

2.1.7 Ear Development

During the period from terminal spikelet formation until anthesis the ear grows rapidly and spikelet differentiation starts from mid part of the ear with formation of florets, progressing towards the tip and base (Kirby 1974; Kirby and Appleyard 1987; Sibony and Pinthus 1988). The phase of spikelet initiation, from collar to terminal spikelet, spans at least 2-3 weeks, but the subsequent development of the spikelet converges such that by the time of terminal spikelet stag each spikelet is at a similar stage, with a number of clearly differentiated florets (Kirby and appleyard 1984). Initiation of florets Continues for several days after the achievement of the terminal spikelet stage up to around the time when the flag leaf has fully emerged (Baker and Gallagher 1983b; Kirby 1988), giving a maximum of 7-12 florets per spikelet (Kirby and Appleyard 1987).

During the subsequent period up to ear emergence, and possibly beyond (Kirby 1988; Siddique et al. 1989), the later formed florets die, leaving 2-6 florets per spikelet. The development of all the surviving basal florets is coordinated such that mieosis is completed by the boot stage, and the male and female gametes mature in time for anthesis, which takes place in all the florets within the space of about 3 days, shortly after ear emergence (Evans et al. 1972, Hay and Kirby 1991).

Under stress Conditions (drought, nutrient deficiency and high density of plant population) all of the florets in the spikelets may show reduced development, and die at a relatively early stage (Langer and Hanif 1973, Hay and Kirby 1991).

The rate of floret initiation is similar in all spikelets and it is varied from 0.2 to 0.4 floret per day (Kirby 1974; Kirby and Appleyard 1987). Ear growth rate increases until the terminal spikelet stage . at this stage the floral shoot apex weighs about 100 mg (Brooking and Kirby 1981; Scartch et al. 1985; Kirby and Appleyard 1987).

More than 99% of the dry mass of the ear is accumulated between terminal spikelet stage and anthesis, at anthesis until end of this period growth rate is similar to that of the stem. Around the time of anthesis the rate of dry matter increase in the ear may fall almost to zero before the grain growth phase starts (Brooking and Kirby 1981). The ear grows from about 3mm long at terminal spikelet stage to 80 mm long until ear emergence (Patrick 1972; Brooking and Kirby 1981).

2.2 Vernalization Response

2.2.1 Introduction

Vernalization in English implies 'springization' through which the winter habit of growth is converted to spring habit. It is only a physiological change and genotype is not changed (Salisbury 1963). It was demonstrated in winter wheat seeds for first time, by the Russian researcher, T. D. Lysenko. who termed that as 'jarovization' meaning summerization in 1928 (Salisbury 1963).

The term 'vernalization' has been defined by Chouard (1960) as "the acquisition, or acceleration, of the ability to flower by a chilling treatment". Napp Zinn (1987) presented two different definitions for vernalization; first; it is a cold treatment that induces or at least promotes flowering, and the second; is the biochemical processes which occur during cold conditions allowing the development of the so-called 'internal conditions' that lead to flower (Napp-Zinn 1987). The development of the 'internal conditions' is governed by two groups of factors: genetic nd environmental factors.

2.2.2 Environmental Influences on Vernalization

2.2.2.1 Low Temperature

Environmental temperature, as well as influencing the rate of growth and metabolism, also plays an important role in controlling the development of plants and hence time of flowering particularly in winter cereals. Winter cereals are unable to flower until they have been vernalized by a period of low temperature. This adaptation improves /the chances of successful reproduction

Kirby and appleyard 1984; Hay and Kirby 1991).

Vernalization response is satisfied by temperatures below 10 °C and the response increases quantitatively from 10 to 0 °C. Different upper limits of vernalization temperature have been reported; e.g 11 °C (Chujo 1966), 12 °C (Vavilov 1951) and 15 °C (Dolgusin 1935). Ahrens and Loomis (1963) found that there is no vernalization effect in winter wheat at -2 °C. Trione and Metzger (1970) support the possibility of an optimum temperature for vernalization with obtaining maximum rate of vernalization at 7 °C while it was much lower at 9° and 3 °C. On the other hand, Weir *et al.* (1984) concluded that temperatures between 3 and 10 °C were fully and effective in bringing about the vernalization of Avalon winter wheat, but the temperatures within the ranges -4° to 3 °C and 10° to 17 °C were less effective. According to Chujo (1966a) higher temperatures (8° to 11 °C) were more favorable for the vernalization of semi-winter wheats, but lower temperatures (4° to 11 °C) were required for strong winter wheats.

There is an interaction between response to tempererature and response to vernalization. Plants develop more quickly at higher temperatures and Low temperatures requiring for vernalization, influence also both the rate of growth and rate of development (Halse and Weir 1970; Kirby and Appleyard 1987). There is no general agreement on the most effective vernalizing temperature and its duration for early induction of flowering.

2.2.2.2 Devernalization Temperature

Devernalization occurred at higher temperatures. Gregory and Purvis (1948) were the first to demonstrate reversal of vernalization with rye variety Petkus by imposing a temperature of 35 °C for 3 days to vernalized seed.
Because of the fluctuation of temperature in the field vernalization in this

conditions must be considered in the context of the effective vernalizing component of diurnal fluctuated temperature and the possible influence of higher (non vernalizing) day temperatures in this process (Flood and Halloran 1986). Chujo (1966b) found that a higher temperature (14° compared with 10 °C) during an 8 hours period required a lower temperature (2° to 6 °C compared with 2° to 10 °C) during the remaining 16 hours of the day for comparable rate of vernalization. Vernalization still occurred with temperatures as high as 25-30 °C imposed for 8 hours when plants were exposed to low temperatures (0-5 °C) for 16 hours, but no vernalization occurred if the higher temperature was imposed for 16 hours with low temperature for 8 hours. The effect of low temperature during 8 hours completely reversed by imposing 30 °C for 16 hours.

Ishihara (1963) found that 30 °C day temperature did not influence vernalization response when night temperature were blow 10 °C, and concluded that devernalization most likely did not occur under field conditions. In the field vernalization response is satisfied as the summation of the individual vernalization and devernalization reactions that may affect its progress (Trione and Metzger 1970).

2.2.2.3 Duration of Vernalization

In most investigations, it is assumed that 6to 8 weeks around 5 °C are sufficient for the full vernalization of most wheat cultivars (e.g. Chujo 1966; Trione Metzger 1970; Davidson et al. 1985; Griffiths *et al.* 1985). But different Period of vernalization as well as different temperatures has been suggested for optimum vernalization. Vavilov (1951) showed that following treatments are the most effective for vernalization in a range of wheats;

Soft grained spring wheats	5-10 days in 10-12 °C

Soft grained spring wheats	5-10 days in 10-12 °C
Hard grained spring wheats	10-14 days in 2-5 °C
Semi-winter wheats (Fcultative)	25-30 days in 5-10 °C
Winter wheats	35-60 days in 0- 5 °C

Weir *et al.* (1984) predicted that the complete vernalization for Avalon which is an extreme winter wheat would be after the accumulation of the equivalent of 41 vernal days (where a vernal day was defined as 24 h, during which the temperature required between 3 and 10 °C but fractions of vernal days were accumulated when the plants were exposed to values outside this range).

Fedorov (1989) demonstrated that different types (winter , alternative) of wheat varieties which originated from the same geographical region, have identical vernalization in the length (duration) and its process conditions. For example winter wheat variety of Mironovskaya 808 (winter), Czech alternative and F_1 plants have same length (duration) of vernalization (45 days).

Gotho (1976) classified Japanese wheats into 7 groups from extreme spring habit to extreme winter habit based on the duration of vernalization requirement which he termed it as the 'degree of vernalization requirement'. Although that classification has been found adequate for the explanation of the ecological; distribution of wheat in Japan. Gotho (1980) concluded that the varietal differences of vernalization requirements in winter wheat are generally controlled by a genetic mechanism which is different from vernalization genes.

2.2.2.4 Short Day Vernalization

The ability of short days to substitute for vernalization or to enhance its effects has been known since the early 1930's (Mckinney and Sando 1933). Short days during early growth can accelerate inflorescence initiation in plants

subsequently transferred to long day. This short day vernalization can replace the need for low temperature vernalization (Evans et al 1975, 1987). Cooper found that short days to be as effective as cold days in hastening the flowering of several wheats. Gott (1961) did not find any evidence of short day vernalization, Krekule suggested that Short days replace cold vernalization in those cultivars in which they inhibit growth. In cultivars which do not become dormant in short day, such as most of those from low latitudes, short days can not replace low temperatures. The optimum temperatures for short day action to range from 13° to 18 °C. No short day effects were apparent at higher temperatures (Krekule 1987).

There are varietal differences for the short day effects, and it is most marked in a subgroup of winter wheat (Hay and Kirby 1991), those varieties that have a prostrate habit of growth and where short days inhibit leaf blade growth (Krekule 1987). Although according to Krekule (1987) whether light acts through modifying the vernalization process or as an alternative control mechanism is unknown, but Evans (1987) pointed that mechanism of short day and low temperature vernalization are distinct and different.

In field conditions in winter wheat area, the effect of short days will tend to be obscured by the association of low temperatures and short day-lengths (Hay and Kirby 1991).

2.2.3 Genetic Basis of Vernalization

According to Pugsley (1971, 1972) the growth habit of wheat is governed by a system of genes, which are responsible for the differences in sensitivity to vernalization.

The various designations have been considered for vernalization genes.

But the symbol Vrn/vrn was proposed for genes controlling spring winter habit from 1973 (McIntosh 1973).

Most of studies on the growth habit of wheat have been concentrated on the three loci Vrn1 Vrn2 Vrn3(Mayestrenko 1974 ; Law *et al.* 1975, 1976; Halloran 1976;). Some of those studies have shown 4 genes Vrn1 to Vrn4 (Singh 1967; Pugsley 1968, 1971, 1972), while others have indicated polygenic control for vernalization response or growth habit (Kuspira and Unrau 1957; Hsu and Walton 1970). Winter wheat varieties carry recessive alleles at all loci. The presence of dominant alleles at one or more loci results in partial or complete inhibition of vernalization requirement, so all spring wheats carry at least one dominant allele on one of these loci.

Many of the 21 chromosomes of wheat have been implicated in control of maturity, earliness (ear emergence in general),and response to vernalization and photoperiod. Chromosome of homoeologous group 5 has strong control over vernalization response (Halloran and Boydell 1967; Law *et al.* 1979; Snape et al. 1979). Vrn1 gene which is the most potent gene for vernalization response is located on long arm of chromosome 5A (Pugsley 1971; Law *et al.* 1975), Vrn3 and Vrn4 were found on chromosomes 5D and 5B respectively (Law et al. 1975; Law 1966; Mystrenko 1980). The presence of another vernalization gene as Vrn_5 on chromosome 7B has been reported by Law (1966) and confirmed by Stelmakh (1987) in a substitution line of Chinese Spring variety Hope.

Another gene for vernalization designated as Vrn_2 is located on chromosome 2B (Mystrenko 1980). However, Law Sutka and Worland (1978), Scartch and Law 1984 did not find any evidence for that. On the other hand a large Photoperiodic effect and a small developmental effect were observed. This suggests that the previously described Vrn_2 is either Ppd_2 or an allel of a gene affecting developmental rate (Worland *et al.* 1987) .

The presence of continuous variation in vernalization requirement and the time of ear emergence in wheat from spring to strong winter habit indicates the action of many genes rather than a small number of genes for vernalization response (Snape *et al.* 1976; Flood and Halloran 1986; Worland *et al.*1987). Pugsley (1971) Concluded that Variation in the vernalization of winter wheat varieties are due to multiple alleles. In a study Carried out using a series of 5A substitution lines into Chinese Spring, the most insensitive Vrn1 allele was found on 5A of an accession of triticum spelta (Law *et al.* 1975).

2.2.3.1 The Association Between Vernalization Genes

The combination of vrn1 vrn2 vrn3 genes confers winter habit. but the presence of even one dominant allele gives spring habit (Pugsley 1971, 1972; Flood and Halloran 1986; Stelmakh 1987). Pugsley (1972) and Gotoh (1979) have reported that Vrn_1 gives complete insensitivity to vernalization.

In progenies segregating for vernalization response, part of the variation in rate of development may be due to dosage effect of vrn genes. For example, in the F_2 of the cross Thatcher (Vrn_1 vrn_2 vrn_3) X Winter Minflor (vrn_1 vrn_2 vrn_3) the spring segregates, Vrn_1 Vrn_1 flowered distinctly earlier than the Vrn_1 vrn_1 segregates (Pugesley 1972).

Although Vrn_1 has been shown to be stronger than Vrn_3 in reducing vernalization response, many studies have shown that the chromosomes carrying these genes (5A and 5D, respectively) exhibit reversal in their relative effects in delaying ear emergence compared with the levels of vernalization which they confer. Snape *et al.* (1979) showed that while chromosomes 5A and 5D exhibited interaction between days to ear emergence and vernalization response, only 5D exhibited epistasis for these characters. Its effect on ear emergence and

vernalization is much greater than that of chromosome 5A (Halloran and Boydell 1967; Law *et al.* 1976; Snape *et al.* 1979). Chromosomes 5A and 5B have also has shown to exhibit interaction in a duplicate manner in influencing days to ear emergence (Law 1972).

In tetraploid wheats vernalization response is attained without the contribution of vrn_3 gene from the D genome (Halloran and Boydell 1976). However, the known vrn loci in the A and B genomes of hexaploid wheat could confer variation for this character at the tetraploid level. Bozzini and Giorgi (1971) found that chromosomes 5A, 2B and 7B in the tetraploid wheat variety Capeiti Promoted earliness and chromosomes 1A, 7A and 5B lateness. In hexaploid wheat chromosomes 1A (Knott 1959; Halloran 1975) and 7A (Halloran 1975; Baht and Goud 1979) have been implicated in the control of winter habit.

2.2.3.2 The Pattern of Gene Action for Vernalization Response

The action of vernalization genes may be cumulative, irregular or threshold in nature (Jedel *et al.* 1986). The cumulative action of vernalization genes which causes a quantitative decrease in the length of the vegetative period has been identified by a number of workers (Levy and Peterson 1972; Halloran 1977; Berry *et al.* 1980). The irregular response is characterized by plateaus and/or increases in the length of the vegetative period which occur with extended cold treatment. Halloran (1977) reported that the pattern of vernalization response in spring wheat cultivars Gabo and Mexico 120 had a plateau from 2 to 5 weeks. Berry *et al.* (1980) described the threshold as an all or nothing response involving vrn_3 and/or vrn4 and cumulative involving vrn_1. These results have been obtained by using days to ear emergence .

A continuous variation of vernalization requirement exist between extreme winter and extreme spring wheat (Riddell and Gries 1958b; Pugsley 1971; Gotoh 1976, 1977, 1979, 1980, 1983). Therefore, classifying of wheat simply into two types, spring and winter, seems to be impossible. Pugsley (1971) assumed that the vernalization requirement of winter wheat cultivars are determined by multiple recessive allels at the Vrn loci. Gotoh (1983) reported that four genes are involved in the genetic variation of degree of vernalization requirement, Vrn3 Ivr1, Dvr1 and Dvr2 . Ivr1 increases the degree of vernalization requirements in the presence of any of the Vrn genes, and Dvr1 and Dvr2 decrease that in the absence of Vrn genes. The genes Ivr and Dvr with small action seem to play more important role than major genes, like Vrn genes in breeding for wheat adaptability (Gotoh 1980, 1983).

2.2.3.4 Duration of Gene Effect for Vernalization

Pugsley (1968, 1971) Concluded that the association of variation in vernalization response with that of leaf and spikelet number indicates that vernalization genes may continue to act after floral initiation. Halloran and Pennell (1982) found some influence of vernalization genes on development beyond floral initiation. Flood and Halloran (1984) vernalized four near isogenic lines of Triple Dirk from 0 to 10 weeks and did not find significant differences in duration from floral initiation to ear emergence between them. Gott (1961) and Halse and Weir (1970) have suggested little or no effect after floral initiation. Accroding to definition of vernalization by Chuard (1960), it is "to accelarat floral induction, therefore any effects beyand nitiation such as spikelet number, time to ear emergence are peliotropic effects of vernalization genes (Flood and Halloran 1986; Worland *et al.* 1987).

2.2.3.5 Evolution of Growth Habit

2.2.3.5 Evolution of Growth Habit

It is a common opinion that winter forms are more ancient and primitive than spring forms (Aamodt 1923, cited by Flood and Halloran 1986), otherwise, winter habit is ancestral to spring habit. It is supported by the fact that many wild progenitors of cereals like diploid species of *Aegilops* and *Triticum* have a winter growth habit (Kihara and Tanaka 1958; Halloran 1967). Spring growth habit has also been found in *T. taushi (Ae. squarrosa*, Tanaka 1956 Tanaka and Yamashita 1957). Some facultative form of *Ae. crassa* were found in Iran and Afghanitan (Tanaka 1959). The Hexaploid wheat received the winter allele sg1 and semi-spring gene sg1 from *Ae. squarrosa* and that Sg1 arose from $Sg1^c$ by mutation at the hexaploid level (Tsunewaki 1966). The acquisition of the winter habit gene from the T. taushii Ae. squarrosa parent gave hxaploid wheat better adaptability to higher latitudes than tetraploid wheat (Tsunewaki 1966, 1968).

Studies of vernalization in diploid wheats (Halloran 1984), tetraploid wheats (Flood and Halloran 1983) and many studies in hexaploid wheats indicate that ranges of variation for vernalization is similar at three levels of ploidy in wheat (Flood and Halloran 1986).

2.2.4 Metabolic Changes During Vernalization

There is very little conclusive information to answer this question, which steps in which biosynthetic sequences are catalyzed by vernalization genes (Napp-Zinn 1987)).

De Silva (1978) compared two isogenoc lines of wheat cv. Triple Dirk which only differed in dominant or recessive form of Vrn1 gene. After 5-6 week of vernalization, the recessive winter form increased the rate of ^{32}P incorporation into phospholipids while the dominant spring form decreased up to

75% . This finding support the idea that the vrn1 gene stimulates the synthesis of unsaturated membrane phospholipids during vernalization (Napp-Zinn 1987).

Profound differences were found in the rate of RNA synthesis in coleoptiles of spring and winter types of wheat at devernalization temperatures (Paldi and Devay 1977).

Promotive effects of Gibberellins were observed at threshold level of chilling treatment (Suge and Yamada 1965). Lin and Stafford (1987), concluded that the C20 GAs (GA 53, GA 44 AND GA19) were present in shoots of the vernalized (flowering) wheat seedlings at somewhat higher levels than that in the non vernalized (rapidly growing) wheat seedlings. Aproximatly levels of the C19 GAs (GA20 GA1 GA3) were lower in the shoots of the the vernalized wheat seedlings than in the non vernalized wheat seedlings. The conversion of GA19 to GA20 (C20 to C19 GAs) may be a rate-limiting step in the vernalized wheat seedlings.

Three distinct phases have been characterized in winter wheat vernalization by using metabolic inhibitors with different spectra of activity. these include inhibitors of respiration and oxidative phosphorylation, nucleic acid and protein antimetabolites and inhibitors of their synthesis (Tan *et al.* 1981).

Li *et al.* (1987), in a study on a winter wheat cv. Nong Da 139, suggested that there are two distinct processes during Vernalization, an earlier one in which low temperature induces a changes in the physiological process and a later one in which development is accelerated; the transition between the 2 processes occurs in the middle of vernalization. protein metabolic inhibitors such as Ethionine and P-Flourophenilalanine interfered with vernalization at the middle stage. After 14 days at 2-4 °C Soluble protein content was double that in the

control and new proteins were detected by gel electrophoresis. these proteins were already present in spring wheat without low temperature treatment.

In general, despite many studies of this type the physiological nature of vernalization and its metabolic processes are not clear enough and many questions are still remain.

2.2.5 Vernalization Response During Growth cycle

During three stages of life cycle of wheat plant, vernalization could be satisfied; during seed germination which was indicated in most of the studies, during plant growth (Gott 1957 Aherns and Loomise 1963) and during seed formation and ripening (immature seed, Ridell and Gries 1958; Singh and Jenner 1983, Kato *et al.* 1990).

Embryo stage is an important factor for vernalization of immature seeds. Chilling requirement had to be started from 9 to 12 days after anthesis in wheat (Kato et al. 1990). While Kostjuncenko and Zaruboilo (quoted in Flood and Halloran 1986) found that in this phase vernalization could occur at temperature as high as 14 °C but Pugsley and Warrington (1979) proposed that 11 °C appear to be the upper limit for vernalization during seed formation.

According to Chujo (1966), the effectiveness of vernalization decreases as plant age, with complete loss of effect after three months. Aherns and Loomis (1963), found that the low temperature for floral initiation in winter wheat may be partially eliminated in older plants. Gott (1957) resulted that wheat was responsive to vernalization in 2 to 44 days old plants, but the older the plant was the shorter was the period of cold treatment necessary for satisfying the

vernalization.

2.2.6 Vernalization Influenced Characters

Vernalization promote earlier floral development and ear emergence by reducing the number of leaves initiated (Davidson et al. 1985). Therefore, the influence of Vernalization can be interpreted more clearly from the results of experiments in which leaf numbers were recorded (Hay and Kirby 1991).

Most developmental studies in wheat have used ear emergence (or flowering time) to measure the strength of vernalization response. It is generally accepted that vernalization affects plant development by slowing floral initiation until the cold requirement of the plant has been satisfied. Using Vernalization insensitive **Vrn1** alleles brought forward ear emergence 11 days in a substitution line of Hobit 'sib'. There is close relationship in wheat between the time from sowing to floral initiation and from sowing to ear emergence.

Since vernalization genes alter the length of time it takes for a plant to develop, it is not surprising to find that they influence other agronomic characters. In a longer growing period of winter wheats compared with spring wheats, pleiotropic effects of Vrn1 increase spikelet number per ear (pugsley 1968; Flood 1983; Kirby 1990), height and plant yields (Worland *et al.*1987). Percentage tiller survival appears to be lower in winter wheats (Simons 1982, Hay and Kirby 1991). Fulfillment of vernalization response may reduce Potential yield with reductions in the final leaf, spikelet and tiller number (Levy and Peterson 1972; Wall and Cartwright 1974).

2.3 Photoperiod Sensitivity

2.3.1 Light

Light is one of the most important environmental factors, regarding to its fundamental role in photosynthesis directly and development indirectly. Light controlled developmental processes are found at all sages of growth from seed germination to induction of flowering (Fitter and Hay 1981). Prevention of flowering of many short day plants can be best achieved by a day-length extension of red light (Rees 1985).

Duration of light varies daily, seasonally and with latitude. Day-length at different times of the year is, for non-tropical organisms, the most reliable indicator for predicting, and hence avoiding, unfavorable conditions, and most plants are photoperiodic (Fitter and Hay 1981).

2.3.2 Photoperiodism

Photoperiodism by definition is a response to change in the length of day, or more accurately night, which is an accurate measure of time, and hence of season, at all latitudes (Rees 1985).

The photoperiodic response enables the plant to time vegetative and floral growth to fit seasonal changes in environment (Fitter and Hay 1981). Day-length response can not be considered in isolation from temperature, because it is rare to find these two wholly independent of each other. Many plants that are day neutral at one temperature are sensitive to day-length at another. In the absence

of prior low temperature treatment, no flowering can occur irrespective of photoperiodic treatment in winter wheats (Rees 1985).

2.3.3 Response to Photoperiod in Wheat

Gott *et al.* (1955) showed on the other member of Gramineae that daylength is perceived by the leaves. In the field, the spring or vernalized winter wheat cannot respond to the prevailing daylength until the first leaf emerges (Hay and Kirby 1991).

Most wheat cultivars are quantitative long day plants and development is faster in long days by reducing leaf number (Evans et al. 1975; Kirby and Appleyard 1987; Levy and Peterson 1972). The quantitative nature of responses of wheats to photoperiod has been established principally by measuring of days to heading (Welsh et al. 1973; Evans 1975; Flood and Halloran 1984; Law 1985; Hay and Kirby 1991).

Several researchers showed this in controled conditions, for example Levy and Peterson (1972) examined a range of cultivars in a glasshouse from 9 to 17 h. For two low latitude cultivars from Mexico increase in daylength from 9 to 17 h caused collar initiation to be advanced one plastochron, giving a reduction of one leaf per main shoot. The other cultivars from a range of including Mexico were more responsive, the increase from 9n to 17 caused collar initiation to be advanced by 6 to 7 plastochron, with a substitutional reduction in number of leaves.

Spikelet development is affected by day-length and the rate of spikelet initiation response strongly increasing by up to 50% if day-length is increased from 8 to 16 h (Holmes 1973; Rahman and Willson 1977). Duration is relatively more affected than rate of spikelet initiation, and the number of spikelets per ear declines with increasing daylength.

2.3.4 Genetics of Photoperiodism in Wheat

Generally the photoperiod sensitive genotypes are delayed in heading by short days, while insensitive genotypes head in a normal time regardless of photoperiod (Welsh et al. 1973; Worland *et al.* 1987). Under comparable conditions, response to photoperiod appears to be vary with the degree of sensitivity of different cultivers.

Response to photoperiod in wheat is controlled by a few major genes which have been designated as Ppd genes (Mcintosh 1973), insensitivity is dominant Ppd and sensitivity is recessive. Pugsley (1965, 1966) suggested that two genes one major and one minor, controlled the inheritance of day-length response in the cross Triple Dirk/Thatcher. Welsh et al. (1973) showd by monosomic analysis that two homoeologous chromosomes 2D and 2B carrying major genes Ppd1 and Ppd2 for photoperiod response respectively. Law et al. (1987) found that in addition to Ppd1 and Ppd2 a third locus, Ppd3, was almost certainly located on chromosome 2A. The multiple alleles effect were demonstrated by Scartch and Law (1984) at the Ppd1 and Ppd2 loci to promote insensitivity.

Scratch and Law (1983) with finding that Ppd1 and Ppd2 are functionally identical and are also located at complete positions on the maps of the two chromosomes, suggested that, Ppd1 and Ppd2 are the same genes, duplicated as a consequence of the polyploid nature of wheat.

2.3.5 The Role *Ppd* Genes in Adaptation

There are strong genotype-environment interactions in the response of varieties to day length (Rahman and Willson 1977; Worland *et al.* 1987) which is extremely important in determining the wide adaptability of wheat (Worland *et al.* 1987). Almost certainly particular Ppd genes have had a decisive effect on the spread of wheat throughout the world.

In northern Europe maximum yield can be achieved by the growing season of winter wheats to nearly a year by delaying flowering with photoperiod sensitive genes. In hot summer conditions cause desiccation and yield losses to late flowering wheats, so plants must carry photoperiod insensitive genes to accelerate flowering and escape drought conditions (Quisenberry 1982; Worland *et al.* 1987; Blum 1988).

Meditranian wheats were used by Norman Borlauge in the early days at CIMMYT, Mexico (Blum 1988)to transfer photoperiod insensitive alleles to the important semi-dwarf wheats of the green revolution. This proved great adaptability undoubtedly because of their daylength.

2.3.6 Affected Characters by *Ppd* Genes

The peliotropic effect of Ppd genes on characters other than time to ear emergence could be valuable to the physiologists in understanding casual relationships and plant processes, and they are very important in crop breeding for adaptation. The effects of Ppd1 versus ppd1 on agronomic characters were studied by Worland and Law (1986). The presence of Ppd1 accelerated flowering by more than 7 days.

Pleiotropic effects of this allele included an 8% reduction in plant height and reduced spikelet number as direct consequences of the shortened period of growth. Grain size also reduced in the presence of Ppd1 and leaded a reduction in overall yield about 5%. They found in southern Europe where summer desiccation is very serious, the benefit of Ppd1 can be very striking. Cultivars carrying ppd1 (recessive) have much reduced grain sizes because of delaying in ear emergence and suffering grain development by high temperatures.

2.3.7 Interactions of Vernalization and Photoperiod in Wheat

However, a spring wheat with a strong photoperiod response can be as late maturing as a winter wheat, and the interaction between these processes in

determining growth habit is considerable.

Vernalization and photoperiod responses determining timing of floral development, are highly significant to wheat's adaptation and hence, yield (Halse and Wair 1970; Halloran 1975; Law 1985 Flood and Halloran 1986). Photoperiod response, can exert an influence on the rate of development prior to floral initiation and can thus exhibit an interaction with vernalization (Flood and Halloran 1984).

These two responses appear to be controlled independently by two separate sets of genes. But they appear to interact physiologically to control flowering (Aitken 1966; Evans *et al.*1975). It has been reported in wheat, as in many long day plants:

Evans *et al.* (1975) pointed that vernalization reduces the need for subsequent long days. Cooper (1960) found that days replaced cold shortening the time from sowing to flowering. This phenomenon is termed short day vernalization (Evans *et al.* 1975; Hay and Kirby 1991).

The significant Interaction between vernalization and photoperiod was found by Levy and Peterson (1972) in controlling days to heading that vernalization could partially substitute for photoperiod. In contrast, Gott (1961) found no evidence for short day vernalization and Halloran (1975) found lack of a significant interaction between these processes.

Flood and Halloran (1984) examined two pairs of isogenic lines of the varieties Triple Dirk and Blackhull and found that vernalization and photoperiod, at least in these cultivars ewre not Physiologically interactive.

Law (1985) pointed that there is no evidence for any interaction between and Vrn genes in their control of time to ear emergence, The additive dominance model is adequate to explain the observed variation. the two sets of genes therefore act independently on this complex character, suggesting perhaps that they may influence different component processes.

2.4 Quantitative Genetic Analysis

Gentic analysis provides an understanding of the way in which different characters are inherited. The first step in the genetic analysis of a characters is to estabilish whether the variation should be considered qualitative or quantitative. This is determined by whether clear, phenotypic classes can be distinguished in segregation, or whether the phenotype forms a continuous range of values.

Genetic variation for most of the characters in wheat that the plant breeder is concerned with is quantitative. Gentic analysis of quantitative characters provides estimates of genetic models in populations of plant. Any single experiment is only a sample the universe, however, to thhat the results estimates from that sample. Any non-representativeness of the sample will lead to bias in the results.

2.4.1 Genetic Analysis of Quatitative Characters

The variation in these characters is continuous and controlled by many loci whose effects combine to produce the observed genotypes (Falconer 1981; Snape 1987). Phenotypic differences between individuals and families in segregating generations are expressed as statistical concepts of a population rather than as frequencies of distinct phenotypic classes. The inheritance of such characters is studied by interpreting these population statistics (means, variances and covariances) in terms of the combined effects of many genes and environment, under defined mating systems.

There is an extensive array of analysis available to wheat geneticists which enable the genetical variation to be partioned and interpreted in terms of

gene action. These are: additive effects, dominance, epistasis, linkage and genotype X environment interaction (Mather 1949; Falconer 1981; Mather and Jinks 1982).

The performance exhibited in any character by a genotype is its phenotypic expression. In order to analyse the genetic properties of a population, the phenotypic value is divided into component parts attributable to different causes. Phenotypic value is determined by genotypic effects and environmental effects, and can be shown symbolically (Falconer 1981, Baker 1986) as follows:

$$P_{ij} = G_i + E_j$$

where P_{ij}, G_i, and E_j represent the phenotypic value, the genotypic value and environmental value respectively, associated with ith individual or line. When there is an interaction (i.e. inconsistency) between genotype and environment, the interaction component would be another source of variation and the model would be:

$$P_{ij} = G_i + E_i + GE_{ij}$$

The amount of variation is measured and expressed as variance. Therefore the total phenotypic variation (σ^2_P) is also partitioned into the variance of genotype (σ^2_G), environment (σ^2_E) and genotype X environment interaction (σ^2_{GE}) as follows:

$$\sigma^2_P = \sigma^2_G + \sigma^2_E + \sigma^2_{GE}$$

The total genotypic variance, σ^2_G can also be further partitioned into components describing the type of gene action:

$$\sigma^2_G = \sigma^2_A + \sigma^2_D + \sigma^2_I$$

where σ^2_A is the additive genetic variance (variance of average allele effects), σ^2_D is the dominance variance (variance of heterozygosits), σ^2_I is the epistatic variance (interlocus non-allelic interaction) consisting of all interactions between dominance and additive effects (i.e. σ^2_{AA}, σ^2_{AD}, σ^2_{DD}).

2.4.2 Phenotypic Analysis and Estimation of Variance Components

A knowladge of genotypic variation is very important in the improvement of quantitative characters. To achieve this in plant breeding, usually a sample of genotypes is grown in a series of environments. Both the lines and environments are considered to be representative of appropriate inference Universe. The total phenotypic variance observed is partitioned into genotypic, genotype X environment interaction and various environmental variance components (see chapter 3). A pooled analysis across all environments provides these estimets in addition to genotype performances (Comstaock and Robinson 1952: Comstock and Moll 1963).

The data should satisfy basic assumptions for a trouble-free analysis. These asumptions have been discussed in detail by Cochran (1947) elswhere. The magnitude of each variance component is calculated from the expectation of the mean squares and the significance is determined by by an appropriate F-test (see chapter 3). The percision of a variance component estimate can be examined by its standard error, according to Crump (1946) as follows:

$$S.E.\sigma^2_t = [2(MS_n)^2/(f_n + 2)]^{1/2}$$

where σ^2_t is the variance component, MS_n is the mean squares in estimating σ^2_t and f_n is the degree of freedom of the n-th square.

2.4.3 Heritability

The heritability is one the most important propeties of a quantitative character. It expresses the proportion of the total variance that is attributable to the main effects of genes (Falconer 1981). There are two differentt meanings of heritability: in the sense that the total genotypic variance is examined, it is called broad sense heritability, and is defined as the ratio of genotypic variance to phenotypic variance:

$$h^2 = \sigma^2_G/\sigma^2_P,$$

where h^2 = heritability

σ^2_G = genotypic variance

σ^2_P = phenotypic variance (sum of all variance component associated with the experimental model.

However, it has already been defined that the genotypic variance can be partitioned into components as follows:

$$\sigma^2_G = \sigma^2_A + \sigma^2_D + \sigma^2_I$$

where:

σ^2_A = variance of average allele effects

σ^2_D = variance of dominance effect

σ^2_I = variance of epistasis effect

The second sense of heritability is concerned with the average genotypic result in a progeny population as transmitted from its parents. This is called narrow sense heritability, and is defined as the ratio of additive genetic variance to the phenotypic variance (σ^2_A/σ^2_P) (Falconer, 1981). In long-term self-pollinated plants (such as wheat) because of inbreeding, the σ^2_D and σ^2_I are trivial, and $\sigma^2_G = \sigma^2_A$ (Falconer 1981). Therefore the ratio of actual genotypic

variance to phenotypic variance in wheat is already narrow sense heritability.

Heritability can be estimated in terms of variance components from replicated plots grown in a number of environments (broad sense), and on the basis of parent-offspring regression technique (narrow sense).
Hansone (1963) has discussed the estimation of heritability using variance components, and the use of parent-offspring regression for estimating heritability was discussed in detail by Robinson *et al.* (1949) and Falconer (1981).

The heritability estimates can be computed in two forms for each character, one using the full phenotypic variance of the model ("full" heritability), and the other using only the single experiment variance components ("restricted" heritability, Gordon *et al.* 1972).

That is,

I. Full heritability, $h^2 = \sigma^2_G/\sigma^2_{P1}$

II. Restricted heritability, $h^{2'} = \sigma^2_G/\sigma^2_{P2}$,

where σ^2_{P1} and σ^2_{P2} were defined as follows:

$\sigma^2_{P1} = \sigma^2_E + \sigma^2_G + \sigma^2_{GE} + \sigma^2_R + \sigma^2_e$ (full phenotypic variance)

$\sigma^2_{P2} = \sigma^2_G + \sigma^2_{GE} + \sigma^2_e$ (restricted phenotypic variance)

where;

σ^2_E = macro-environment variance

σ^2_{GE} = genotype X environment interaction variance

σ^2_R = block variance (meso-environment)

σ^2_e = error variance.

The full heritability estimates the genotypic variation as a fraction of total phenotypic variance. The restricted type has been more commonly used in the

literature (Allard, 1960), and is more appropriate when the phenotypic performance of two genotypes are compared within the same block at a particular site.

The standard errors of heritability estimates are determined according to Gordon et al. (1972). The variance of a ratio (e.g. Z=X/Y) is computed as follows:

$$\sigma^2 = [\mu^2_y \sigma^2_x + \mu^2_x \sigma^2_y - 2\mu_x\mu_y \text{Cov}(x,y)]/\mu^4_y$$

Where $\mu_y = E(y)$; $\mu_x = E(X)$; σ^2_x, σ^2_y and σ^2_z are variances of x, y and z respectively. The factors x, y, z Correspond to σ^2_G, σ^2_P and h^2 in the heritability equation. The σ^2_x, σ^2_y and Cov(x,y) are also calculated using the estimator of Gordon et al. (1972).

2.4.4 Genotypic and Phenotypic Correlation

A knowledge of the association between characters is valuable to plant breeders because it may lead a breeder to plan a more efficient selection program. According to Falconer (1981), the correlation which is directly observed is a compound of genetic and environmental causal components (phenotypic correlation). The genotypic correlation is a correlation amongst genotypic effects only. A significant genotypic relationship indicate either pleiotropic effects of the same genes or linkage of genes controlling the separate characters.

The genotypic and phenotypic variance and covariances can be used to estimate the genotypic (r_g) and phenotypic (r_p) correlations among the various traits (Falconer, 1981; Baker, 1986) as follows;

$$r^g = \frac{cov_{G(ij)}}{(\sigma^2_{Gi}\sigma^2_{Gj})^{1/2}}$$

$$r^p = \frac{cov_{P(ij)}}{(\sigma^2_{Pi}\sigma^2_{Pj})^{1/2}}$$

where;

$cov_{G(ij)}$ = genotypic covariance component

$cov_{P(ij)}$ = phenotypic covariance component

σ^2_{Gi} and σ^2_{Pj} = genotypice variance component of traits i and j respectively.

σ^2_{Pi} and σ^2_{Pj} = phenotypic variance component of traits i and j respectively.

Many published examples of phenotypic correlations between characters in wheat have been obtained from studies of samples of varieties. However, significant correlations do not necessarily imply a functional relationship. Also they may be completely fortuitous because of the sample chosen (Snape 1987). Estimating of the genetic co-relationships by using the genetic covariance seems to be a more appropriate approach. The actual estimation of covariances is analogous to estimation of variances (Snape 1987).

2.4.5 Genotype X Environment Interaction

Phenotype reflects non-genetic as well as genetic influences on development. The phenotypic response to a change in environment may vary from genotype to genotype. This inter-play (inconsistency) in effect of the genetic and non-genetic on effects on development is called genotype X environment interaction (Comstock and Moll, 1963). Genotype X environment

interaction becomes very important when a genotype is to be used in a range of environmental conditions. Variation in response due to inconsistency of the interaction of genotype with environment is an intrinsic part of genotypic behaviour and its estimation is important for the assessment of a variety.

The existence of genotype X environment interaction has been concern to plant breeders for a long time. It has been reviewed by Comstock and Moll (1963), Hill (1975), Freeman (1973) Westcott (1986), elsewhere. Several methods are used in the case of wheat, but the application of only two multivariate techniques, principal component analysis and cluster analysis are reviewed briefly in the following.

2.4.6 Principal Component Analysis

Multivariate techniques may be used to describe the performance of genotypes by considering the environment as an attribute (or variables) and genotypes as entities. Principal component analysis defines linear combinations of the attributees $x_1 \ldots, x_p$ rather than the attributes themselves (Cooly and Lohnes 1971). Applying principal component analysis, the variables (here environments) are combined and the total variance is explained by producing as many components as the number of variables.

According to Morrison (1967) generally the few first components describe most of the variance in data. The first principal component explain the maximum of variance, and the second principal component explain the maximum of remaining variance and so on. The principal components are independent of each other (Westcott 1986; Becker and Leon 1988).

The chief difficulty with this method is the interpretation of resulting principal components, which may not bear any obvious relationship to

environments (Westcott 1986). Interpretation of the meaning of components is on the basis of factor structure matrix which indicates the correlation of each variable with each of the components. If the correlations between a component and environments are of a similar level it will describe the general effects of environment on the examined traits. Otherwise it would be represented as an interaction. The first component indicates usually the general effects and the others may show contrast between variables (Morrison 1967). Genotypes are characterized by their principal component values. Genotypes with a large principal component scores would be positioned in the extreme low or extreme high level of performance, depending on the correlation between its relevant component and environmens (Becker and Leon 1988).

2.4.7 Cluster Analysis

Cluster analysis is the method of classification and allocation of individuals into groups (Everitt 1974; Lin *et al.* 1986). The aim of using this analysis is to assign the genotypes into quantitatively homogeneous subsets (groups, clusters). The variation amongst groups is large after clustering. If attributes are GE responses and entities are genotypes, the clusters may vary importantly due to the differing genotye responses to environment (Lin *et al.* 1986; Backer and Leon 1988).

A number of workers have used cluster analysis to classify wheat genotypes and environments (Byth *et al.* 1976; Brennan *et al* 1981). There are several methods for clustering genotypes based on similarity of response characteristics. Comerack (1971), listed eight different sorting strategies and 10 different similarity measures. The choice of these affect the particular clusters which result.

Lin *et al.* (1986), divided the smilarity measures to two major classes: uni-

criterion and multi-criterion. Four groups has been reported for uni-criterion measure: (1) Euclidean distance, (2) standardized distance, (3) dissimilarity index, (4) correlation coefficient. There are two types of index for each group: type (a) indicates the similarity using both genetic effect and G X E interaction, and type (b) indicates the similarity based on G X E interaction alone.

In contrast to uni-criterion clustering, in multi-criterion procedures, developed by Lefkovitch (1985), permit more than one measure of pairwise relationship to be used. Lefkovitch defined dissimilarity of genotypes by three measures: the mean over all enviroments, the variance across environments, and among-environments patterns. Genotypes can be grouped using all measures either sequentially or simultaneously to decide on group homogeneity.

Determination of a number of usful clusters is still main difficuty of this analysis. Anderberg (1973) suggested that the normal way is to make a subjective choice according to previous knowledge of the data. Gordon (Pers. com.) and Teow (1978) applied a cut-off point based on the F-ratio of amongst cluster sums of square/within cluster sums of squares.

Chapter 3

MATERILS AND METHODS

The study was carried out under natural conditions during 1990/1991 at Palmerston North, New Zealand (latitude, 40° 23'S). The spring-winter habit of the growth of 43 genotypes of wheat have been studied under different conditions of temperature and photoperiod (environments). The different regimes of temperature and photoperiod were provided by changing the sowing date which will be described later.

3.1. The Objectives of the Research:

1. to investigate the responses of growth habit traits to different environments (temperature and day length) in order to investigate selection criteria for growth habit in field;

2. to estimate descriptive heritability of the traits from phenotypic variance components;

3. to estimate phenotypic and genotypic correlations between the growth habit characters;

4. to estimate and categorize the genotype-environment interactions in the growth habit characters;

5. to re-consider what is meant by growth habit in wheat;

6. to investigate the effects of environment and genotype on the timing of development of wheat;

7. to screen this germplasm for:

   a. presence and magnitude of putative vernalization and photoperiod responses, and subsequently for spring-winter habit of growth,

   b. general maturity .

3.2. Plant Material

Plant material consisted of 43 genotypes (lines) of common wheat (Triticum aestivum L.) differing for earliness and growth habit, and diverse in origin and genetic background. Eight Lines were registered as commercial cultivars in New Zealand, England, Australia and South Africa; namely Batten, Otane, Oroua, Karamu, Rongotea, Transval, Konini, Genero 81, and Avalon. Avalon is widely grown in England and is a strong winter type used in crop simulation and vernalization studies (Kirby et al. 1984, 1987; Delecolle and Hay 1989). The other 35 genotypes are advanced lines of Crop Research Division of DSIR, New Zealand, and cover a range of "winter" and "spring" types. A list of the genotypes used in this study and some descriptions of them is presented in Table (3.1) and thier pedigree of breeding are also presented in Apendix (3.1).

Table 3.1 The studied wheat genotypes, their origins and putative habit specifications :

Genotype:	Origin	Putative Type	Maturity
Batten	New Zealand	winter	Medium
C7205 (CRAW 17)	France	winter	Medium
PBI 1908-49-5	England	winter	M e d i u m
P648-05 (CRAW 50)	New Zealand	winter	Late
PBI 1908-49-7	England	winter	Mid-late
C3640	France	winter	Late
P693-02	New Zealand	winter	M e d i u m
PBI 1013-13-3	England	winter	Mid-late
3431-01	New Zealand	winter	Mid-late
3458-34	New Zealand	winter	Early
3494-01	New Zealand	winter	Medium
88PBI9	England	winter	M e d i u m
Avalon	England	winter	Late
CR3-135	New Zealand	winter	Late
CR3-136	New Zealand	winter	Late
CRAW 45	New Zealand	winter	Medium
PBI 1641-25	England	winter	Late
3415-20	New Zealand	winter	Medium
3410-10	New Zealand	winter	Late
3413-09	New Zealand	winter	Late
Konini	New Zealand	winter	Medium
3496-03	New Zealand	winter	Medium

Table 3.1 continued.

Genotype:	Origin	Putative Type	Maturity
3665-30	New Zealand	winter	Medium
3665-08	New Zealand	winter	Medium
Otane	Mexico(CIMMYT)	spring	Early
CR5/188 (PSW 251)	New Zealand	spring	Early
CRSW 6 (PSW 251	New Zealand	spring	Late
CRSW 18	New Zealand	spring	Medium
CRSW 19	New Zealand	spring	Early
CRSW 22	New Zealand	spring	Medium
Genero 81	Mexico(CIMMYT)	spring	Early
18-IBSWN	Mexico(CIMMYT)	spring	Early
P694,03	New Zealand	spring	Early
Oroua	New Zealand	spring	Early
Karamu	Mexico(CIMMYT)	spring	Early
Rongotea	New Zealand	spring	Late
Otane Rogue	New Zealand	spring	?
Transvaal	South Africa	spring	?
Sout Africa 1116	south Africa	spring	Early
659/16	New Zealand	spring	Early
449.02.22	Oroua/65.09	spring	early
441,021	New Zealand	spring	?
722,02	New Zealand	spring	Late

3.3. Environmental Conditions

It was noted in the Review of Literature that growth habit of wheat is a function of response to vernalization and photoperiod. Therefore, the environments in this study is sampled seasonal variation in temperature and phootoperiod, during the growth cycle. Different enviroments were provided by changing sowing dates; 26-June, 3-Aug, 21-Sep and 4-Dec. Figures 3.1 and 3.2 show the variation of soil and air temperature and daylength in these environments. Other environmental factors, such as soil and fertility properties, water availability and crop management, were as constant as possible for all genotypes and environments.

3.4. Experimental Design

A randomized complete block design with two blocks was used in each sowing date. Each plot consisted of one row with approximately 50 plants in each plot after thinning. The plots were 2.2 m. in length with 30 cm. row spacing. Inter plant spacing was 5 cm.. There were also single guard rows on each side of the block. In the fourth sowing date, a length of 60 cm. was added to each row to sow vernalized seeds of the respective lines in order to record vernalization response.

3.5. Crop Management

3.5.1. Sowing

The plants were sown in silty loam soil in a field which had been fertilized prior to planting with compound fertilizer, 15 kg/ha P and 30 kg/ha N . Cultivation consisted of mouldboard ploughing, and followed by seed bed preparation using rotary-hoe and hand hoe to get the seed bed as even as

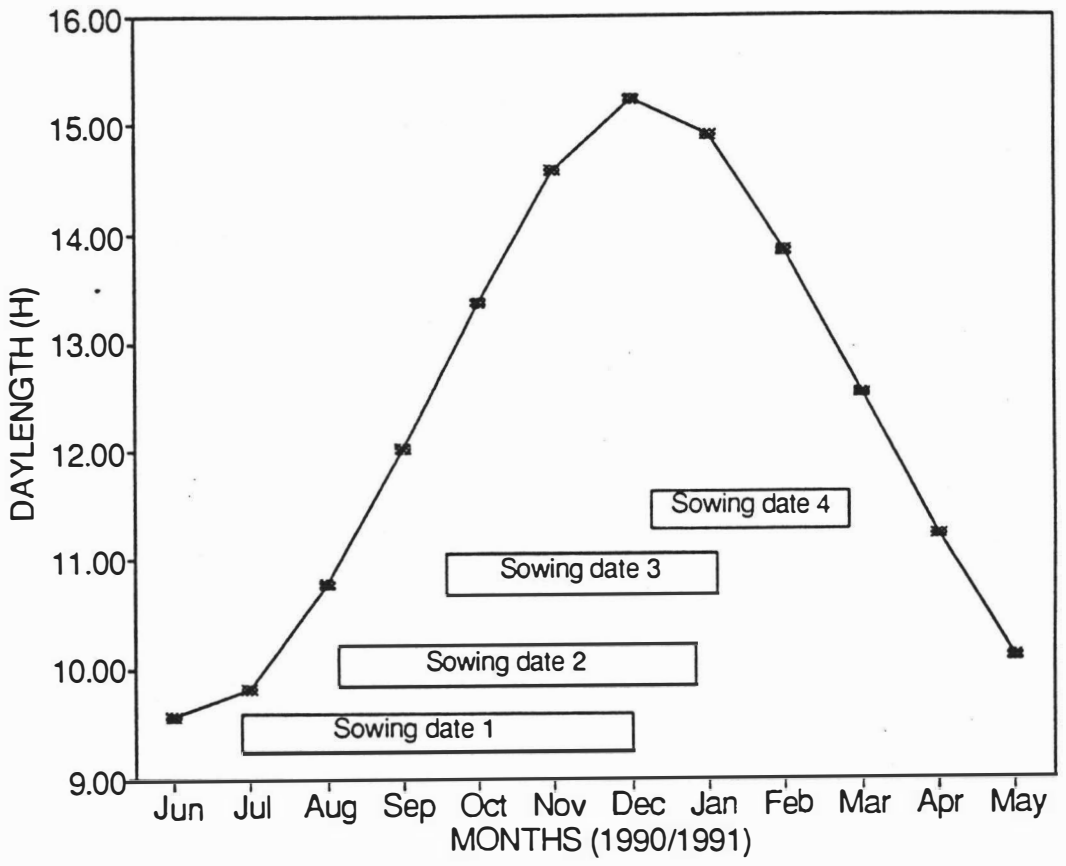


Figure 3.1 Day-length changes during growth in different sowing dates (Environments). Each Box represents The time from sowing to to the last anthesis for each sowing date.

Source of data: Grasslands, DSIR (E05363, Palmerston North, DSIR).

Figure 3.2, Changes of temperature during growth in each environment.

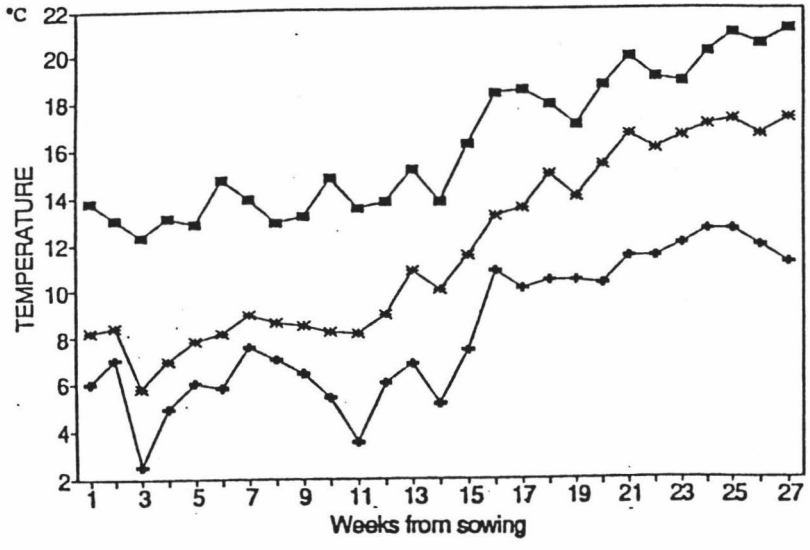
—■— Weekly average of Max. air temperature.

—●— Weekly average of Min. air temperature.

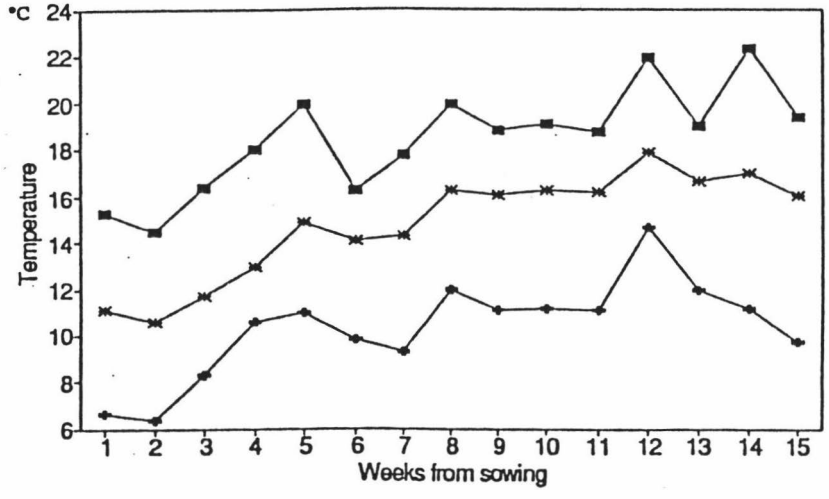
—✱— Weekly average of mean soil temperature.

Source of data: Grasslands, DSIR (EO5363, Palmerston North, DSIR).

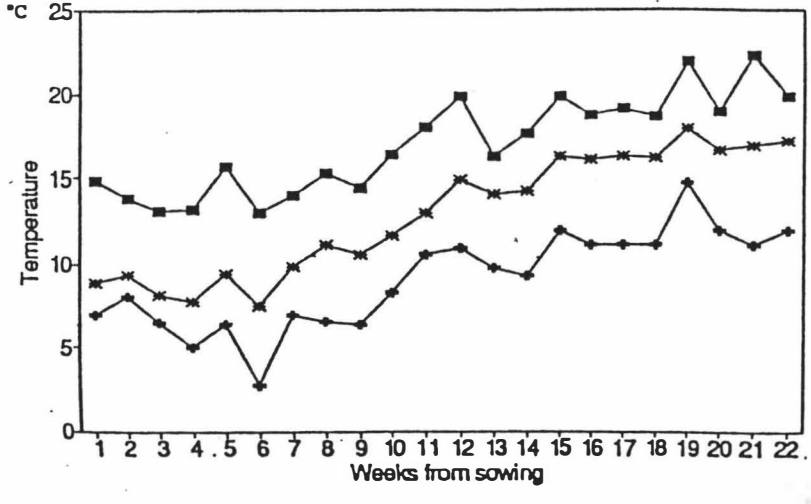
Environment 1



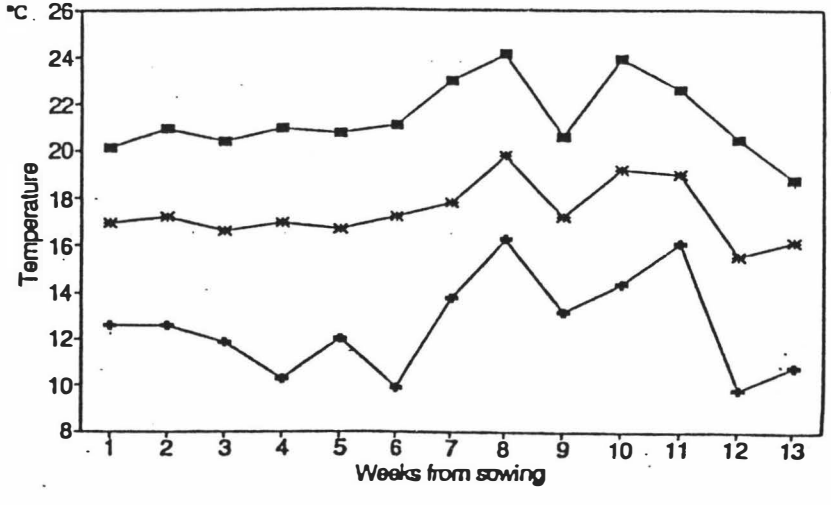
Environment 3



Environment 2



Environment 4



possible. Sowing was done with a precision plot seeder for sowing dates one and four; but wet weather necessitated hand sowing for second and third sowing dates. The sowing depth in all sowings was 5-6 cm. All plots were uniformly top dressed with urea giving 70 kg nitrogen per hectare at the third leaf stage. Irrigation was not necessary in this region, but to prevent any stress during a relatively dry period in summer, sprinkler irrigation was done for sowing dates 3 and 4 before flag leaf stage.

3.5.2. Thinning and Weed Control

The plants were thinned to approximately 5 cm. inter plant spacing. Thinning was done before full emergence of the third leaf.

Since plant apical development was being studied, no herbicide was applied to control the weeds. Weeding was done mechanically by hand several times during the growing period.

3.5.3. Pests and Diseases Control

Experiments were sprayed with fungicide Folicar (2.5 ml/litre) 2-3 times, to control diseases (specifically yellow rust). The third experiment was attacked by Hessian fly (Mayetiola destrutore Say.) in early stages, when most plants consisted only of the main tiller. In spite of spraying regularly with the insecticides, Metasystox (1 ml/litre) and Vydate (4 ml/litre), the prime tillers died in most of the plants. For the forth experiment granule form of pesticide 'Furadan G ' was applied during seeding to control Hessian fly .

3.5.4. Tagging

All of the characters were measured on single plant basis, and most of them were recorded on the main (first) tiller. Therefore, ten plants per plot were tagged randomly as internal replications for measuring leaf and flowering characters. A subset of these plants (the 5 random plants with odd numbers)

were used for other characters. Tagging was done at the third leaf stage, since recognition of main tiller is easy when the third leaf is fully emerged (Kirby and Appleyard 1984). Brightly coloured tags (telephone wire) were placed on the most recently fully-emerged leaf on the main tiller, and the number of the tagged leaf was recorded. Leaves were numbered from the oldest to youngest leaf (from the ground upwards). At the second time of leaf counting, new leaves were counted upwards from the old tagged leaf to last visible leaf. Then tags were relocated to the most recent fully emerged leaf at this time, and the new leaf numbers were recorded.

3.6. Characters Measured.

3.6.1 Leaf Appearance.

(a). The visible leaf tips on main tiller were recorded on tagged plants after the third leaf stage. Leaf appearance was recorded on the basis of the Haun scale (Haun 1973). The last partially emerged leaf was estimated as a proportion of the last fully emerged leaf. The number of emerged leaf tips were expressed as the umber of fully emerged leaves + the previously mentioned proportion of last partially emerged leaf.

(b). The number of fully emerged leaves (only) was recorded also.

(c). The repositioning of the tags (section 3.5.4) enabled leaf appearance to be recorded three times during growth, at 3 to 4 week intervals in the winter sowings (experiments 1 and 2), and at two week intervals in the spring sowings (experiments 3 and 4).

These data were used subsequently to estimate (by regression) the leaf appearance rates in these liness.

3.6.2 Final Leaf Number.

The third count actually provided the number of total leaves produced on main tiller. According to Hay and Kirby (1991) the study of Vernalization response and photoperiod sensitivity using leaf number is more precise than using flowering time.

3.6.3 Tiller Production.

The line differences in tillering pattern, and in the numbers of tillers, were studied by counting tillers three times during the growth. Tillers were counted at the same time as were leaves counted. Tiller number was counted on the 5 plants subset per plot, mentioned earlier.

These data were used subsequently to estimate tiller production rate for given genotypes, using regression analysis.

3.6.4 Total Tillers per Plant

The third tiller count provided the number of total tillers produced by plant during growth. This count was done at anthesis time. All of tillers including leafy and dried tillers were counted using the 5 plant subset.

3.6.5 Number of Fertile Tillers per Plant.

The number of fertile (grain bearing) tillers was recorded also for the 5 individual subset plants (section 3.5.4). A fertile tiller was a tiller bearing a spike at the stage of grain filing (soft-dough stage).

3.6.6 Fertility Ratio of the Tillers

This character was estimated by dividing the number of fertile tillers by number of total tillers. This propotion of fertile tillers may vary due to growth habit and genotype (Flood 1983; Flood and Halloran 1986; Hay and Kirby 1991). Winter types are expected to have a smaller ratio than spring types, particularly in the later sowings.

3.6.7 Days from Sowing to Flag Leaf Emergence.

Days from sowing to ful emergence of the flag leaf were recorded on the main stem of the 10 tagged plants per plot. For this purpose the earlier plots were checked at 2 to 3 days interval. When the final leaf (flag leaf) was observed fully emerged, with its ligule, the date of the emergence was recorded. Days from sowing to flag leaf emergence were calculated on a single plant basis.

3.6.8 Days from Sowing to Heading

The time of ear emergence or heading was recorded on the main stem of the tagged plants. The date of heading was recorded when the basal spikelets were just fully emerged from the flag leaf sheath. The recorded dates were converted to days from sowing.

3.6.9 Days from Sowing to Anthesis

Anthsis time of the main spike was recorded on the ten tagged plants. When about 50% of the anthers in main spike had released their pollen, the date was recorded. This was converted later to days from sowing.

3.6.10 Spikelet Number per Spike

The number of spikelets on the spike of the main stem was counted after anthesis and was recorded for each tagged plant in the plot. All fertile and sterile spikelets were recorded for this purpose, including the terminal spikelet.

3.6.11 Main Stem Height

The height of main stem was measured individually using the 5 plant subset. The length between the lowest visible node and the base of the spike (basal spikelet) was measured in millimetres. Main stem height is one the characters responsive to temperature and photoperiod (Flood and Halloran 1986; Worland *et al.* 1987). The relationship between this trait and growth habit in these environments was to be considered.

3.6.12 Peduncle Length

The length of the peduncle may respond to temperature and daylength independently of total height. The length of the peduncle was measured in millimetres from the last node up to the base of the ear (basal spikelet).

3.6.13 The Number of Elongated Internodes

Prior to stem elongation internodes are compressed above the crown. When the temperature and photoperiod requirements of the plant are satisfied, upper internodes are elongated and become visible (Kirby and Applyard 1984, 1987: Hay and Kirby 1991). It was desired to examine the relationship between the number of elongated internodes and growth habit. The number of visible internodes (minimum 10 mm length) were counted for the 5 plant subset per plot.

3.6.14 Vernalization Response.

Vernalization response here, was quantified as a difference in days to flag leaf unfolding of unvernalized and vernalized plants of a genotype. It was estimated in whole plot average.

3.7 Statistical Analysis

3.7.1. Nature of the Data

Data were collected from the 43 genotypes of wheat on the basis of individual plant samples for all characters. Some of these were collected from 10 plants per plot, while others were from 5, as mentioned earlier. The collected data can be divided into four types with respect to their structures:

1. Serial data: the data from leaf appearance and tiller production were collected periodically three times during thr growth cycle. Leaf appearance was recorded on all 10 tagged plants and tiller production on the 5 odd number subset in each plot.

2. The timing data (days from sowing to flag leaf, days from sowing to ear emergence, days from sowing to anthesis), number of leaves and the number of spikelets were recorded once on each of the 10 plants per plot.

3. The data for total tiller number, fertile tiller number, main stem height, peduncle length and the number of internodes were measured once on 5 individual plants per plot.

4. The data for days to flag leaf emergence in vernalized plants, were recorded once on the basis of whole plot average in the fourth sowing date. This

was to be used to estimate the vernalization response in relation to the average days to flag leaf in unvernalized plants.

The data on reproductive characters were not collected on some winter types which did not flower in the last two "spring" sowings. The lines were classified therefore into a separate group on this basis. This meant that the full set of genotypes was a vailable for only the two earlier experiments.

To facilitate this problem, the pooled analysis of variance was carried out on two sets of data:

(I). 37 genotypes (flowered in all environments) over 4 environments.

(II). All the genotypes in two "winter" environments.

The data for leaf number, leaf appearance and tiller production were not available in environment 3 became at the Hessian fly attack mentioned earlier (section 3.5.3). These characters, therefore, were to be pooled over 3 environments.

3.7.2. Regression Analysis of Serial Data;

Regression analysis was carried out to study the pattern of leaf appearance and tiller production and their functional relationship against time. These regressions were done separately for each plot. The best fit for each attribute was found after considering the coefficients of determination and the plots for two models:

(a). linear $Y = \beta_0 + \beta_1 X$

(b). exponential $LnY = \beta_0 + \beta_1 X$

where Y = relevent plot data, X = days (from sowing)

Any linear function of variates with normal distributions is also normally distributed (Morrison, 1967), and the regression coefficients are linear function of the data (Draper and Smith 1966). Therefore, estimated intercepts (β_0) and rates (β_1) for the chosen model are normal if the data are normal. Consequently, they were utilised as extra variates in pooled analysis of variance to which all other attributes were subjected.

3.7.3 Single Analysis of Vernalization Response;

The difference in days to flag leaf unfolding of unvernalized and vernalized plants for all genotypes was analysed in a single Randomized Complete Block design with two blocks. The results provide an indirect evaluation of vernalization response in the field conditions.

3.7.4. Pooled Analysis of Variance;

Prior to any pooled analysis plot means of within plot samples (internal replications) were obtained, and analysis was done on them. An appropriate model of pooled randomized complete block design was used in this study as follows:

$$X_{ijk} = \mu + \alpha_i + \beta_{j(k)} + \tau_k + \alpha\tau_{(ik)} + \varepsilon_{(ijk)}$$

Where;

X_{ijk} = the phnotypic observation of ijk-th plot

i = 1,...,g number of genotypes

j = 1,...,b „ „ replications (blocks)

k = 1,...,e „ „ environments;

μ = the grand mean,

α_i = the i-th genotype effect

$\beta_{j(k)}$ = the j-th block effect nested within the k-th environment,

τ_k = the k-th environment effect,

$\alpha\tau_{ik}$ = the ik-th genotype X environment interaction effect

ε_{ijk} = the ijk-th residual error effect.

The sources of variation, Expectations of mean squares and F-tests are presented in Table (3.2), (Steel and Torie 1981). The expectations of mean squares were obtained following Crump (1946). All effects were considered to be random in this analysis. The appropriate F-tests were applied to test the significance of the variance components according to Crump (1946), Satterthwaite (1946) and Le Clerg et al. (1962), such that the F-ratios numerator expectation differed from the denominator only by the variance component being considered. When the numerator or denominator was a linear function of mean squares, a complex F-test resulted (Sattethrwaite 1946; Crump 1946). Satterthwaite derived the appropriate degree of freedom for this test as follows:

$$f' = \frac{[\sum_{1}^{n} (MS_i)]^2}{[\sum_{1}^{n} (MS_i)]^2/f_i}$$

where MS_i is the i-th mean square and the f_i is the degree of freedom associated with i-th meansquare. The computer program THWAITE (Gordon unpublished) was used to estimate the complex F-test for Environment significance test, together with its degrees of freedom according to Satterthwaite.

The computer program SAS (Anon 1988) was employed for the analysis of variance including degrees of freedom, and significance tests using the equations and formulas indicated in Table (3.2). Duncan multiple range and LSD methods were used for means comparison.

The variance components were estimated from the expectations of the mean squares (Table 3.2). Program THWAITE supplied these, together with their standard errors.

Table 3.2 Sources of variation, degrees of freedom, expectations of mean squares* and F-ratios of environmental pooled analysis

S.O.V	DF	Ms	E(MS)	F-Ratio
Environment	e-1	MS_E	$\sigma^2 + g\sigma^2_{B(E)} + b\sigma^2_{GE} + bg\sigma^2_E$	$(MS_e + MS_E)/MS_B + MS_{GE})$
$Block_{(Env.)}$	e(b-1)	$MS_{B(E)}$	$\sigma^2 + g\sigma^2_{B(E)}$	MS_B/MS_e
Genotype	g-1	MS_G	$\sigma^2 + b\sigma^2_{GE} + be\sigma^2_G$	MS_G/MS_{GE}
G X E	(g-1)(e-1)	MS_{GE}	$\sigma^2 + b\sigma^2_{GE}$	MS_{GE}/MS_e
Error	e(g-1)(b-1)	MS_e	σ^2	

* Random effects philosophy.

3.7.5. Estimation of Genetic Variability

Variance component estimates were obtained from linear functions of the mean squares as indicated by their expectations (Table 3.2). Standard error of variance components were also computed following Crump (1946) and Satterthwaite (1946), to evaluate the precision of these estimates.

The computer program THWAITE was used to estimate the variance components and their standard errors.

3.7.6. Estimation of Heritability

The heritability (h^2)in the broad sense is the ratio of genotypic variance (σ^2_G) to phenotypic variance (σ^2_P) (Falconer 1981).

$$h^2 = \sigma^2_G/\sigma^2_P$$

where $\sigma^2_P = \sigma^2_E + \sigma^2_G + \sigma^2_{GE} + \sigma^2_R + \sigma^2_{er}$

and:

σ^2_E = environment variance

σ^2_{GE} = genotype X environment interaction variance

σ^2_R = block variance

σ^2_{er} = errore variance

Genetic variance could also be partitioned to its components as follows:

$$\sigma^2_G = \sigma^2_A + \sigma^2_D + \sigma^2_I$$

where:

σ^2_A = variance of average allele effects

σ^2_D = variance of dominance effect

σ^2_I = variance of epistasis effect

The ratio of σ^2_A/σ^2_P expresses the heritability in the narrow sense. As wheat lines are long term self-pollinated plants, dominance variance is trivial, as are epistasis variance involving dominance. Therefore $\sigma^2_G = \sigma^2_A$ and the estimated heritability in case is narrow sense heritability.

The heritability estimates were computed in two forms for each character: "full" heritability, using the full phenotypic variance of the analysis and the "restricted" heritability, using only the single experiment variance components (Gordon *et al.* 1972).

I. Full heritability = σ^2_G/all variance components

II. Restricted heritability, $h^2 = \sigma^2_G/\sigma^2_G + \sigma^2_{GE} + \sigma^2_{er}$

The restricted type has been more commonly used in the litrature (Allard, 1960), and is more appropriate when the phenotypic performance of two genotypes are compared within the one experiment.

3.7.7. Genotypic and Phenotypic Correlations

A knowledge of the association between characters is valuable to plant breeders because it may help the breeder to plan a more efficient selection program. According to Falconer (1981) the correlation which is directly observed is a compound of genetic and environmental causal components (Phenotypic correlation). The genotypic and phenotypic variance and covariances can be used to estimate the genotypic (r_G) and phenotypic (r_P) correlations among the various traits (Miller *et al.* 1953; Falconer 1981; Baker 1986) as follows;

The phenotypic correlation coefficients were estimated as simple correlation coefficients on the basis of plot means of two sets of data: (a) 37 genotypes in 4 environment, (b) 43 genotypes intwo winter environments. "Proc Corr" as implemented in computer program SAS was used to compute these estimates.

Partitioned sums of squares and cross-products with the pooled model, were obtained using procedure GLM in SAS. The genotypic correlations were estimated using the genotypic partitions.

3.7.8. Principal Component Analysis of G X E Interactions

The characters showing significant genotype X environment interaction were used to characterize the responses of these genotypes across the four environments. As there were growth and development attributes resulting from varying responses to vernalization and photoperiod, these patterns may reveal categories of plant habit. The analysis was done on standardized means.

The un-rotated structure of each analysis was used to interpret the meaning of component solutions in each character's analysis. Standardized component scores were then estimated for each character for each line, in order to indicate the plants form to which the line belonged. In order to minimize the number of principal components utilized for each attribute (parsimony) it was decided to use only those components which accumulated at least 70% of the variances in the GE means (see chapter 2).

3.7.9. Cluster Analysis

Following the principal component analysis, the parsimony criteria led to two scores being used for each attribute, making fourteen scores for each line. This led to a new data set still too complex to comprehend, although, in this form, it would be the best possible discriminator set for identifying plant habit. Therefore, a cluster analysis was done on the principal component scores, in order to recognize the groups of plant habit which had been defined.

A data matrix for clustering consisted of two principal component scores for each of seven attributes, for each genotype, as described already.

The similarity matrix was based on Eucledian distance, and the Ward method of clustering was used in subsequently. In this method minimal increase of within-cluster sum-of-squares is the criterion of merging. At each step of the analysis, union of every possible pair of clusters is considered and two clusters the fusion of which results in the minimum increase in the error sum-of-squares, are combined. The computer program 'SPSSx' was employed to run the cluster analysis.

A dendogram was produced showing the hierarchical result of this agglomerative clustering analysis.

3.7.10 Post-cluster Analysis

Two analysis of variance were carried out after clustering. The first was a

MANOVA using the original attributes to determine the cut off level in the dendogram, thereby defining the useful number of clusters. The second consisted of a series of ANOVA, for each cluster and attribute and principal component score, in order to define the mean properties of each cluster.

The truncation point was defined as that point in the progressive clustering where amongst-cluster variances (of the attributes) were most significant compared to within-cluster variances. The cluster analysis reported genotype membership of clusters at several successive stages. Each of these was used to define "treatments" in successive MANOVA, one for each stage. Rao's F-approximation of Wilk's lambda were used to get a joint significance test of all attributes simultaneously. That clustering stage which had greatest significance was used as the cut-off point (Gordon, pers. com.; Teow, 1977; Cullen, 1982).

Following a decision about the cluster definition (see above) simple analyses were carried out separately for each attribute to describe the mean attribute of each cluster. The principal component scores were averaged similarly, cluster by cluster.A simple analysis of variance was carried out to provide F-test, and means comparison of all chosen clusters for each character. The clusters were summarized thereby to define the growth habit of genotypes in each cluster.

Chapter 4

RESULTS

Different techniques of analysis were employed to study the data and results presented here include:

1. Rate analysis of leaf appearance and tiller production.

2. Single analysis of vernalization response

3. Quantitative genetic analysis:
    a) Genetic variance and heritability analysis
    b) Correlation analysis of all characters:

The pooled analysis of variance for this latter purpose was carried out in two seprate sets. Analysis (a) included 37 genotype over all 4 environments and excluded the strong winter types which did not flower in spring sowings. Analysis (b) included all 43 genotypes over the two winter environments.

4. Analysis of genotypic performance for studied characters:
    a) general genotypic performance;
    b) performance of genotypes in environments.

5. Response pattern analysis:
    a) principal component analysis;
    b) cluster analysis.

The abbreviations used to refer to the characters and their units of mesurement are presented in Table 4.1.

Table 4.1 The abreviations used to refer to the characters and their unit of measurement

Characters	Abbreviation	Unit
Leaf appearance rate	LAR	Leaf tip/day
Tiller production rate	TPR	Log(tiller/day)
Final Leaf number	LFN	No.
Days to Flag Leaf unfolding	DFL	Day
Days to heading	DHD	Day
Days to Anthesis	DANT	Day
The spikelet number per spike	SPKN	No.
Fertile tillers number	FTN	No.
Total tillers number	TTN	No.
The fertility ratio of tillers	FRAT	Ratio
Main stem height	MSH	mm
Peduncle length	PL	mm
Internodes number	INTN	No.

4.1. Estimation of Leaf Apprearance and Tiller Production Rates.

The serially collected data were regressed plot by plot against time to obtain the slopes of regression lines, that is the rates of leaf appearance and tiller production. First of all, in order to ascertain which model of two (linear or exponential) effected best fit for each character, the coefficients of determination

of each was estimated for each plot.

Table 4.2 indicates the occurrences of best fits for each function for each character, using the coefficient of determination. The decision was to use linear for leaf appearance and exponential for tiller production.

The rates of leaf appearance and tiller production (slopes of regression lines) of genotypes were subjected to a pooled analysis of variance over 3 environments (these traits were not recorded in experiment 3, see chapter 2). The results of this analysis including variance components, heritability, genotypic means and G X E means will be presented later in sections 4.2 and 4.4.

Table 4.2 The comparison of coefficints of determination of linear and exponential functions in 3 experiments as indicated by the numbers of best fits (largest R^2's).

Model	Exp1	Exp2	Exp4
Leaf Appearance:			
Linear	83	58	36
Exponential	13	35	60
Tiller Production:			
Linear	28	25	49
Exponential	68	71	47

4.2. Single analysis of vernalization test

Time to flag leaf emergence in vernalized seeds and unvernalized seeds were compared in fourth sowimg date as described in chapter 3, in order to determine the vernalization response of this germplasm. The response is expressed in terms of magnitude of the difference between the two times of flag leaf emergence (Unver. - Ver.). Higly significant genotypic variation was observed for this character (Table 4.3). The vernalization responses of all genotypes are presented in Table 4.4.

Six genotypes have shown very strong response such that they have not flowered in the third and fourth sowing dates. Genotype CROW 45 was very responsive (15 days) and classified in first class on the basis of Duncan 5% significant level. Assumed spring genotypes Genero 81, Otane Rouge and No. 41 were in second class of vernalization response (8.5 - 9.5 days).

Table 4.3 Analysis of variance for vernalization response.

Source	MS	F-test	Sig.
block	0.888	0.50	ns
genotype	34.18	19.26	**
error	1.77		
C.V.=63.14%	$\bar{x}$ = 2.74		

Table 4.4 Vernalization responses of 43 genotypes of wheat, on the basis of difference in time to flag leaf emergence between unvernalizd and vernalized seeds;
(Duncan's multiple range test)

Genotype	Response (unv.-ver.)	Significance group
Avalon	NF	
C3640	NF	
CR3/135	NF	
CR3/136	NF	
3410-10	NF	
3413-09	NF	
Batten	0.0	fghij
C7205 (CRAW 17	11.5	b
PBI 1908-49-5	-0.5	fghij
P648,05(CRAW 50)	2.0	efg
PBI 1908-49-7	0.0	fghij
P693,02	-0.5	fghij
PBI 1013-13-3	1.0	fghi
3431-01	-1.5	ij
3458-34	-1.0	hij
3494-01	2.0	efg
88PBI9	0.0	fghij
CROW 45	15.0	a
PBI 1641-25	-2.0	i

NF = No flowering in sowing date 3 and 4

Table 4.4 continued

Genotype	Response (unv.-ver.)	Significance group
3415-20	-0.5	fghij
Konini	4.5	de
3496-03	1.5	fgh
3665-30	8.0	c
3665-08	7.0	cd
Otane	0.5	fghij
CR5/188(PSW 251)	3.5	f
CRSW 6(PSW 251	1.0	fghi
CRSW 18	-1.0	hij
CRSW 19	-0.5	fghij
CRSW 22	0.0	fghij
Genero 81	9.0	bc
18-IBSWN-136	9.5	bc
P694,03	-1.0	hij
Oroua	0.0	fghij
Karamu	1.0	fghi
Rongotea	0.5	fghij
Otane Rogue	8.5	c
Transvaal	0.0	fghij
S.F.A 1116	1.5	fgh
659/16	-0.5	fghij
449,02/22	-0.5	fghij
441,021	-1.5	ij
722,02	1.5	fgh

Means with same letter are not significantly different at 5% level.

4.3 Quantitative genetic analysis of genotypes and environments

The results of the two sets of pooled analyses (analyses of 37 genotype over 4 environments and 43 genotype over 2 environments) will be compared for general values, environmental and genotypic means, phenotypic and genotypic correlations. The importance of sampling of environments and genotypes in this kind of studies will be discussed in chapter 4.

The centeral values of the attributes grand means and thier coefficients of variation for each attributes are presented in Table 4.5. Most of the attributes have low coefficients of variation (< 10%) which indicated a high level of precision in the pooled experiments.

4.3.1. Magnitude and Significance of Variance component estimates

Biometrical mean squares were partitioned to estimates of variance components of environment, block, genotype, interaction of genotype and environment and error. Variance component stimates of analysis (a) and analysis (b) are presented in Tables 4.6 and 4.7 respectively.

4.3.1.1 Environmental effects

Plant phenotypic performance is a function of the environmental effect and genotypice characteristics. Environmenmental effects in this study were - estimated by the variance components of: Environment, Block and Error. Most of the studied attributes, except the number of total tillers, showed highly significant environmental variances (Table 4.6 and Table 4.7).

Table 4.5 Central values (grand means), coefficients of variation and units of each character.

Attribute	Analysis (a) C.V.	Analysis (a) $\bar{x}$	Analysis (b) C.V.	Analysis (b) $\bar{x}$
DFL	1.61	82.97	1.04	113.28
DHD	1.50	97.64	1.05	129.60
DANT	1.42	101.86	0.92	133.80
LFN	2.31	9.95	2.51	10.94
SPKN	3.42	20.98	3.08	22.57
FTN	21.31	5.82	23.08	6.30
TTN	19.33	8.98	17.84	9.23
FRAT	13.65	0.668	12.37	0.71
MSH	6.48	735	7.02	771
PL	7.20	334	7.35	337
INTN	5.41	5.33	5.43	5.68
LAR	5.16	0.126	*	*
TPR	24.32	0.0243	*	*

Analysis (a): 37 genotypes over 4 environments

Analysis (b): 43 genotypes over 2 environments

* Characters LAR and TPR, were the rates (slops) of leaf appearance and tiller production in regression analysis which all genotypes were included in that analysis. Therefore analysis (b) has not been done for these characters.

Table 4.6 Variance component estimates, their standard errors (in brackets) and their significances for pooled analysis of 37 genotypes over four environments.

Attribute	V_{Res}	V_E	V_B	V_G	V_{GE}
DFL	1.78	1141.41	0.44	41.90	19.08
	(0.21)	(722.37)	(0.27)	(10.78)	(2.69)
		**	**	**	**
DHD	2.16	1267.79	0.23	49.84	14.77
	(0.25)	(802.17)	(0.17)	(12.35)	(2.14)
		**	**	**	**
DANT	2.09	1286.54	0.17	42.21	12.73
	(0.24)	(813.97)	(0.13)	(10.48)	(1.86)
		**	**	**	**
LFN	0.053	1.379	0.0073	0.446	0.530
	(0.0072)	(0.987)	(0.002)	(0.149)	(0.092)
		**	ns	**	**
SPKN	0.51	3.58	0.06	2.29	0.93
	(0.06)	(2.30)	(0.04)	(0.59)	(0.16)
		**	**	**	**
FTN	1.63	0.65	0.18	0.49	0.02
	(0.19)	(0.49)	(0.13)	(0.16)	(0.15)
		**	**	**	ns

V_{Res}, V_E, V_B, V_G and V_{GE} are: residual, environment, block, genotype, genotype X environment variances respectively.
$p < 0.01 = **$, $0.01 < p < 0.05 = *$, $p > 0.05 = ns$

Table 4.6 continued.

Attribute	V_{Res}	V_E	V_B	V_G	V_{GE}
TTN	3.02	0.08	0.69	2.06	0.27
	(0.35)	(0.37)	(0.44)	(0.58)	(0.30)
		**	**	**	ns
FRAT	0.0083	0.0052	0.0015	0.0084	0.0032
	(0.0097)	(0.0039)	(0.0011)	(0.0024)	(0.0011)
		**	**	**	**
MSH	2244.1	9040.1	267.9	9258.7	352.3
	(262.6)	(5828.1)	(189.8)	(2209.2)	(238.3)
		**	**	**	ns
PL	579.0	699.4	61.0	2089.3	211.1
	(67.8)	(463.6)	(4.3)	(508.3)	(75.5)
		**	**	**	**
INTN	0.083	0.207	0.004	0.041	0.027
	(0.010)	(0.133)	(0.003)	(0.014)	(0.010)
		**	*	**	**
LAR(10^{-4})	0.42	6.10	3.50	0.06	0.104
	(0.53)	(4.43)	(0.23)	(0.23)	(0.61)
		**	**	ns	**
TPR(10^{-4})	0.35	2.4	0.14	-0.02	0.28
	(0.48)	(1.75)	(0.63)	(0.05)	(0.12)
		**	*	ns	**

Table 4.7 Variance component estimates, their standard errors (in brackets) and their significanses for pooled analysis of 43 genotypes over two enviroments.

Attribute	V_{Res}	V_E	V_B	V_G	V_{GE}
DFL	1.393	116.73	0.074	102.94	4.97
	(0.212)	(33.93)	(0.075)	(22.55)	(1.21)
		**	*	**	**
DHD	1.846	135.56	0.051	106.96	6.416
	(0.22)	(110.84)	(0.066)	(25.56)	(1.57)
		**	ns	**	**
DANT	1.528	148.95	0.222	86.02	5.310
	(0.233)	(121.82)	(0.182)	(19.00)	(1.30)
		**	**	**	**
LFN	0.075	0.259	-0.002	1.607	0.277
	(0.011)	(0.217)	(0.0003)	(0.377)	(0.067)
		**	ns	**	**
SPKN	0.464	1.608	0.018	3.688	0.686
	(0.071)	(0.848)	(0.021)	(0.889)	(0.198)
		**	ns	**	**

V_{Res}, V_E, V_B, V_G and V_{GE} are: residual, environment, block, genotype, genotype X environment variances respectively.
$p < 0.01 = **$ $0.01 < p < 0.05 = *$ $p > 0.05 = ns$

Table 4.7 continued

Attribute	V_{Res}	V_E	V_{Blk}	V_G	V_{GE}
FTN	2.115	0.945	0.245	0.214	0.199
	(0.322)	(0.901)	(0.208)	(0.224)	(0.312)
		**	**	*	ns
TTN	2.713	0.493	-0.061	2.250	1.703
	(0.414)	(0.436)	(0.010)	(0.869)	(0.684)
		**	ns	**	**
FRAT	0.0076	0.0023	0.0018	0.0148	0.0041
	(0.0012)	(0.0023)	(0.0014)	(0.0041)	(0.0018)
		**	ns	**	**
MSH	2935.65	3136.75	277.31	11281.23	-14.82
	(447.68)	(2704.73)	(244.23)	(2564.77)	(382.19)
		**	**	**	ns
PL	612.96	157.49	89.011	2304.15	118.03
	(93.96)	(176.81)	(73.05)	(538.40)	(101.86)
		**	**	**	ns
1NTN	0.0954	0.0602	0.0053	0.0620	0.0282
	(0.0145)	(0.0528)	(0.0053)	(0.0227)	(0.0177)
		**	*	**	*

Large environmental componentss were obtained particularly for leaf appearance and tiller production, days to flag leaf emergence, ear emergence and anthesis. Block variance was not significant in this analysis. It indicates that characters were more responsive to temperature and photoperiod than block conditions (such as soil fertility).

4.3.1.2 Genotypic Variance

Genotypic effects are involved in genotypic and genotype X environment variance components. These components were generally highly significant. As described earlier (chapter 1 and chapter 2, growth habit is actually an interactive performance of genotype and environment rather than either genetical or environmental alone. Therefore, the variance component of genotype X environment interaction was the most important indicator component in this study, and it was highly significant for characters DFL, DHD,DANT, LFN, SPKN, FRAT,LAR and TPR, and was significant for TTN, PL, INTN.

Characters FTN, MSH, have shown non-significant G X E interction variance (Table 4.6 and Table 4.7). Genotypic variance for leaf appearance and tiller production rates was very low (compare to their environment variance) and the observed variance in those rates was mostly due to the Environment.

4.3.2 Heritability Estimates

The heritability estimates (both terms of full heritability and restricted) are presented for all studied characters in Tables, 4.8 and 4.9. All heritabilities presented here are narrow sense heritability, because all the genotypes were long-term self-pollinated with trivial dominance variance (chapter 2 and 3).

Table 4.8 shows the heritabilities estimated by analysis (a), pooling 37 genotypes over 4 evironments. Many of the characters were affected largely by environments. Therefore, they have shown low heritabilities.

Table 4.8

Heritability estimates and their standard errors obtained from pooled analysis of 37 genotypes in 4 enviromments;

Attr.	h^2	Se	$h^{2'}$	Se
DFL	0.035	0.003	0.670	0.026
DHD	0.037	0.003	0.750	0.022
DANT	0.031	0.002	0.740	0.024
LFN	0.185	0.157	0.433	0.275
SPKN	0.132	0.049	0.613	0.109
FTN	0.166	0.124	0.230	0.156
TTN	0.340	0.097	0.680	0.156
FRAT	0.315	1.439	0.422	1.450
MHN	0.457	0.002	0.780	1.376
PL	0.574	0.004	0.725	0.030
INTN	0.113	0.31	0.270	0.620
LAR	0.0076	0.059	0.101	0.781
TPR	0.0006	0.024	0.032	0.134

h^2=full heritability

$h^{2'}$=restricted heritability

Se=standard error

Characters DFL, DHD and DANT had lowest heritability amongst the studied characters (about 3%). The full heritability was low for characters LFN, SPKN, FTN, and INTN (11-18%) and it was medium for TTN, FRAT, MSH and PL (31-57%). Although characters DFL, DHD and DANT have shown very low full heritability, they had high level of restricted heritability about 67-74% (Table 4.8). The restricted heritability was also high for MSH, PL, TTN and SPKN (61-78%), and it was medium for LFN and FRAT (42-43%), and low for FTN and INTN (23-27%). This is because, the restricted estimate ignored the purely environmental variances of environments and blocks, as is usual.

The heritability estimates of studied characters obtained by analysis (b) of 43 genotypes over only two winter environments are given in table 4.9. Those characters which had a very low level of full heritability in analysis (a) were mostly in a medium to high level of full heritability in this analysis.

On the one hand, reduction in range of environments (from four environments, sowing from early winter to early summer, to only two winter environments) reduced the environment variance component. On the other hand, increasing in the number of genotypes from 37 to 43 increased the genotypic variance component. Consequently the heritability was increased in the analysis with a larger number of genotypes and narrower range of environments. Characters DFL, DHD, DANT, TTN and FRAT had medium level of heritability (32 - 48%) with this range of environments and genotypes.

The full heritability was high for characters LFN, SPKN, MSH and PL (63-72%), but it was low for INTN 25% and very low for FRAT 6%. Restricted heritability in this analysis was very high for characters DF, DHD, DANT and LFN (82-94%), high for SPKN, MSH, and PL (76-79%), medium for TTN, FRAT and INTN (33-56%) and very low for FTN 8.5% (Table 4.9).
The relevance of these trends to wheat habit will be discussed subsequently.

Table 4.9

Heritability estimates and their standard errors obtained from pooled analysis of 43 genotypes over two environments.

Attr.	h^2	Se	$h^{2'}$	Se
DFL	0.455	0.067	0.942	0.010
DHD	0.426	0.021	0.928	0.011
DANT	0.355	0.020	0.926	0.013
LFN	0.724	0.196	0.820	0.132
SPKN	0.630	0.030	0.760	0.092
FTN	0.058	0.125	0.085	0.180
TTN	0.317	0.112	0.338	0.115
FRAT	0.483	1.640	0.558	1.570
MSH	0.640	0.031	0.794	0.014
PL	0.700	0.042	0.759	0.034
INTN	0.247	0.558	0.334	0.664

h^2=full heritability

$h^{2'}$=restricted heritability

Se=standard error

4.3.3 Phenotypic and Genotypic Correlation

Phenotypic and genotypic correlations for all pairs of characters were estimated in the two different sets (a , b). Table 4.10 presents the phenotypic correlation estimated by set of 37 genotypes and 4 environments (set 'a'). Genotypic correlation estimated through the partitoned pooled model of this set, are given in Table 4.11. There was a very high level of phenotypic correlation as well as genotypic correlation between the characters DFL, DHD, DANT (about 0.98 - 0.998), and this indicates that these chraracters in fact might be essentially one character. Phenotypic and genotypic correlations between these characters and LFN were also very high (0.80 - 0.84).

There was a high phenotypic (0.70 - 0.76) and moderate genotypic (0.48 - 0.65) correlation between SPKN and above mentioned characters. The phenotypic correlation between characters LAR and TPR and those flowering characters DFL, DHD and DANT was negatively high, while the genotypic correlation between them was very low and non significant. The genotypic correlation between TTN and flowering characters and leaf number was high, but phenotypic correlation between them was low to moderate. The character FRAT had negatively high genotypic correlation with flowering characters, leaf number and tiller number and negative moderate with spikelet number. However, the phenotypic correlation between FRAT and those characters was negatively low to moderate. Correlation between other pairs of characters, either phenotypic or genotypic, were low to moderate.

Phenotypic and genotypic correlations estimated by the set of 43 genotype and 2 environments (set b) are presented in Tables 4.12 and 4.13 respectively. The correlations between flowering characters in this analysis were similar to those in analysis (a), as indicated in the following.

Table 4.10 Phenotypic correlations considering 37 genotypes in 4 environments.

Attribute	DFL	DHD	DANT	LFN	SPKN	FTN	TTN	FRAT	MSH	PL	INT	LAR
DHD	0.998 **											
DANT	0.998 **	0.999 **										
LFN	0.816 **	0.810 **	0.803 **									
SPKN	0.707 **	0.710 **	0.703 **	0.763 **								
FTN	0.345 **	0.347 **	0.356 **	0.361 **	0.324 **							
TTN	0.154 **	0.150 **	0.144 *	0.450 **	0.316 **	0.520 **						
FRAT	0.247 **	0.254 **	0.270 **	-0.031 **	0.034 **	0.476 **	-0.462 **					
MSH	0.414 **	0.415 **	0.428 **	0.345 **	0.280 **	0.438 **	0.564 **	-0.082 ns				
PL	0.16 **	0.161 **	0.176 **	0.082 ns	0.072 ns	0.362 **	0.574 **	-0.194 **	0.852]**			
INTN	0.662 **	0.662 **	0.668 **	0.506 **	0.455 **	0.322 **	0.415 **	-0.026 ns	0.603 **	0.332 **		
LAR	-0.807 **	-0.807 **	-0.812 **	-0.589 **	-0.566 **	-0.348 **	-0.386 **	-0.027 ns	-0.570 **	-0.373 **	-0.661 **	
TPR	-0.787 **	-0.793 **	-0.798 **	-0.545 **	-0.549 **	-0.390 **	-0.440 **	-0.017 ns	-0.594 **	-0.844 **	-0.658 **	0.692 **

$p < 0.01$ = **, $0.01 < p < 0.05$ = *, $p > 0.05$ = ns

Table 4.11 Genotypic correlations considering 37 genotypes in four environments.

Attribute	DFL	DHD	DANT	LFN	SPKN	FTN	TTN	FRAT	MSH	PL	INTN	LAR
DHD	0.998 **											
DANT	0.981 **	0.997 **										
LFN	0.840 **	0.813 **	0.822 **									
SPKN	0.650 **	0.661 **	0.675 **	0.480 **								
FTN	-0.026 ns	-0.059 ns	-0.032 ns	0.145 ns	-0.043 ns							
TTN	0.807 **	0.775 **	0.792 **	0.765 **	0.480 **	0.373 **						
FRAT	-0.870 **	-0.861 **	-0.863 **	-0.705 **	-0.543 **	0.347 **	-0.722 **					
MSH	-0.480 **	-0.488 **	-0.422 **	-0.320 *	-0.310 *	0.377 **	-0.273 *	0.570 **				
PL	-0.561 **	-0.567 **	-0.530 **	-0.300 *	-0.282 *	0.387 **	-0.367 **	0.671 **	0.914 **			
INTN	-0.220 ns	-0.222 ns	-0.205 ns	-0.288 *	-0.240 *	-0.043 ns	-0.237 *	0.261 *	0.410 **	0.340 **		
LAR	0.082 ns	0.087 ns	0.082 ns	-0.072 ns	0.222 ns	-0.130 ns	-0.080 ns	-0.058 ns	-0.123 ns	-0.135 ns	0.071 ns	
TPR	0.106 ns	0.100 ns	0.049 ns	0.220 ns	-0.098 ns	-0.147 ns	0.083 ns	0.192 ns	-0.152 ns	-0.037 ns	-0.007 ns	-0.115 ns

$p < 0.01$ = **, $0.01 < p < 0.05$ = *, $p > 0.05$ = ns

Table 4.12 Phenotypic correlations considering 43 genotypes in 2 environments.

Attribute	DFL	DHD	DANT	LFN	SPKN	FTN	TTN	FRAT	MSH	PL	INTN	LAR
DHD	0.995 **											
DANT	0.990 **	0.993 **										
LFN	0.840 **	0.832 **	0.805 **									
SPKN	0.710 **	0.706 **	0.702 **	0.645 **								
FTN	0.229 **	0.234 **	0.279 **	0.168 **	0.269 **							
TTN	0.625 **	0.610 **	0.600 **	0.690 **	0.524 **	0.558 **						
FRAT	-0.455 **	-0.432 **	-0.372 **	-0.571 **	-0.306 **	0.406 **	-0.505 **					
MSH	-0.183 *	-0.179 *	-0.100 ns	-0.344 **	-0.123 ns	0.348 **	-0.148 ns	0.538 **				
PL	-0.348 **	-0.349 **	-0.270 **	-0.464 **	-0.243 **	0.275 **	-0.233 **	0.569 **	0.871 **			
INTN	0.125 ns	0.132 ns	0.167 *	-0.001 ns	0.085 ns	0.283 **	-0.003 ns	0.312 **	0.435 **	0.230 **		
LAR	-0.339 **	-0.341 **	-0.384 **	-0.103 ns	-0.101 ns	-0.320 **	-0.107 ns	-0.255 **	-0.179 *	-0.254 **	-0.25 *	
TPR	-0.105 ns	-0.110 ns	-0.148 ns	0.004 ns	-0.008 ns	-0.158 *	-0.039 ns	0.236 **	-0.163 *	-0.142 ns	-0.142 ns	0.053 ns

$p < 0.01$ = **, $0.01 < p < 0.05$ = *, $p > 0.05$ = ns

Table 4.13 Genotypic correlations considering 43 genotypes in 2 environments.

Attribute	DFL	DHD	DANT	LFN	SPKN	FTN	TTN	FRAT	MSH	PL
DHD	0.996 **									
DANT	0.996 **	0.997 **								
LFN	0.902 **	0.900 **	0.901 **							
SPKN	0.750 **	0.744 **	0.755 **	0.658 **						
FTN	-0.046 ns	-0.056 ns	-0.036 ns	0.062 ns	0.078 ns					
TTN	0.812 **	0.798 **	0.803 **	0.800 **	0.608 **	0.382 **				
FRAT	-0.902 **	-0.892 **	-0.885 **	-0.785 **	-0.512 **	0.244 *	-0.788 **			
MSH	-0.548 **	-0.556 **	-0.511 **	-0.543 **	-0.366 **	0.245 *	-0.394 **	0.567 **		
PL	-0.630 **	-0.640 **	-0.595 **	-0.586 **	-0.404 **	0.238 *	-0.440 **	0.635 **	0.915 **	
INTN	-0.202 ns	-0.192 ns	-0.184 ns	-0.180 ns	-0.158 ns	-0.014 ns	0.265 *	0.300 *	0.315 *	0.231 ns

$p < 0.01$ = **, $0.01 < p < 0.05$ = *, $p > 0.05$ = ns

There was a high level of genotypic and phenotypic correlation between flowering character and LFN (0.80 genotypic and 0.90 phenotypic), SPKN (0.70 in both), TTN (0.85 genotypic and 0.65 phenotypic). FRAT had very high negative genotypic correlation (0.90) and moderate negative phenotypic correlation (0.40) with flowering characters.

The genotypic correlation between FRAT and TTN was negatively high and phenotypic correlation was negative moderate. Character PL had moderate negative correlation with flowering characters, LFN, SPKN and TTN, and moderate positive correlation with FRAT and very high with MSH.

The relevance of these in understanding plant habit will be discussed subsequently.

4.4 Analysis of genotypic responses

4.4.1 Genotypic general performance

Genotypic grand means represent the general performance of genotypes across all environments. To investigate the possible differences in general performance between wheat types suggested by Flood and Halloran (1986), Kirby Appleyard (1987), the comparison of genotypic means is important. It is also valuable for wheat breeder to find the range of genotypic variation and the supperiority of the examined genotypes in adaptive and agronomic characteers such as general maturity, spikelet number, tiller number etc.. The means were compared for significance differences by Duncan mhltiple range test (Table 4.14) at 55 level of significance.

Six genotypes did not flower in the spring environments, and they were not compared quantitatively. The timing of development in putative sping types was faster than in winter types in terms of DFL, DHD, DANT. Genotypes with

Table 4.14 Comparison between genotypic means (over 4 environments) **(Days to flag leaf unfolding and Days to heading).**

Genotypes	DFL Mean(days)	DFL Sig.group	DHD Mean(days)	DHD Sig.group
Avalon	N.F.		N.F.	
C3640	N.F.		N.F.	
CR3/135	N.F.		N.F.	
CR3/136	N.F.		N.F.	
3410-10	N.F.		N.F.	
3413-09	N.F.		N.F.	
Batten	83.03	fghijk	98.18	fghij
C7205 (CRAW 17	92.26	b	106.66	bc
PBI 1908-49-5	91.35	bc	105.70	bcd
P648,05(CRAW 50)	91.60	b	106.42	bc
PBI 1908-49-7	87.67	cbdef	104.15	bcde
P693,02	87.37	bcdefg	103.46	bcdef
PBI 1013-13-3	88.31	bcde	104.26	bcde
3431-01	89.43	bcde	105.00	bcd
3458-34	83.72	efghij	98.35	fghij
3494-01	86.98	bcdefgh	101.09	cdefgh
88PBI9	89.70	bcd	105.67	bcd
CRAW 45	00.12	a	114.52	a
PBI 1641-25	91.00	bc	107.30	b
3415-20	88.14	bcdef	104.62	bcde
Konini	85.62	cdefgh	100.37	defgh
3496-03	87.09	bcdefg	101.64	cdefg
3665-30	89.60	bcde	103.96	bcde
3665-08	84.79	efghij	100.66	defgh
Otane	73.15	o	87.37	o
CR5/188(psw 251)	3.07	o	87.73	no
CRSW 6(psw 251	82.96	fghijkl	96.32	ghijkl
CRSW 18	80.16	ijkl	93.92	ijklm
CRSW 19	73.37	o	87.62	o
CRSW 22	81.75	ghijkl	96.23	ghijkl
Genero 81	74.81	mno	89.00	mno
18-IBSWN-136	4.43	no	89.00	mno
P694,03	78.66	jklmn	93.21	ijklmn
Oroua	78.45	klmno	91.85	klmno
Karamu	74.55	no	87.47	o
Rongotea	82.06	fghijkl	97.17	ghijk
Otane rogue	74.96	mno	89.02	mno
Transvaal	74.77	no	88.48	mno
S.F.A 1116	74.02	no	87.75	no
659/16	77.73	klmno	92.42	klmno
449,02/22	77.12	lmno	90.94	lmno
441,021	81.03	hijkl	95.69	hijkl
722,02	84.92	defghi	99.32	efghi
S.e.	3.16		2.81	

Means with same letter are not significantly different at 5% level.
N.F.: No flowering in environments 3 and 4.

Table 4.14 Continued **(Days to anthesis and the number of spikelet)**

Genotypes	DANT Mean(days)	Sig. group	SPKN Mean(no.)	Sig. group
Avalon	N.F.		N.F.	
C3640	N.F.		N.F.	
CR3/135	N.F.		N.F.	
CR3/136	N.F.		N.F.	
3410-10	N.F.		N.F.	
3413-09	N.F.		N.F.	
Batten	101.84	ghij	19.62	klmn
C7205 (CRAW 17	110.09	bc	22.10	defg
PBI 1908-49-5	109.67	bcd	24.23	ab
p648,05(CRAW 50)	110.00	bc	23.90	ab
PBI 1908-49-7	107.71	bcde	23.06	abcd
P693,02	106.88	bcdef	20.91	fghijk
PBI 1013-13-3	107.78	bcde	23.79	abc
3431-01	108.81	bcd	22.36	cdef
3458-34	102.52	fghij	20.85	fghijk
3494-01	105.29	cdefgh	22.91	abcde
88PBI9	108.87	bcd	21.51	efghi
CRAW 45	117.72	a	22.83	bcde
PBI 1641-25	110.74	b	24.42	a
3415-20	108.04	bcde	21.66	defgh
Konini	104.53	defgh	18.29	n
3496-03	105.60	cdefg	20.20	hijkl
3665-30	106.95	bcde	19.43	klmn
3665-08	104.58	defgh	21.63	defgh
Otane	91.75	o	19.17	mln
CR5/188(PSW 251)	92.57	no	19.97	jklm
CRSW 6(PSW 251	101.53	ghijkl	21.66	defgh
CRSW 18	98.31	ijklm	20.08	ijklm
CRSW 19	92.20	o	20.59	ghijkl
CRSW 22	100.55	ghijkl	19.93	klm
Genero 81	94.39	mno	19.91	klm
18-IBSWN-136	94.22	mno	19.57	klmn
P694,03	97.51	jklmn	20.83	fghijk
Oroua	96.30	klmno	18.63	mn
Karamu	91.88	o	19.56	klmn
Rongotea	101.58	ghijk	9.73	klmn
Otane rogue	94.71	mno	18.58	mn
Transvaal	93.48	mno	20.91	efghij
S.F.A 1116	93.44	no	20.32	hijkl
659/16	96.67	klmno	21.46	efghij
449,02/22	95.96	lmno	20.47	hijkl
441,021	99.94	hijkl	20.52	hijkl
722,02	103.89	efghi	20.45	hijkl
Se	2.62		0.77	

Means with same letter are not significantly different at 5% level.

Table 4.14 Continued **(Final leaf number)**

Genotypes	Mean(no.)	Sig. group
Avalon	N.F.	
C3640	N.F.	
CR3/135	N.F.	
CR3/136	N.F.	
3410-10	N.F.	
3413-09	N.F.	
Batten	10.12	bcefdgh
C7205 (craw 17	11.26	ab
PBI1908-49-5	11.09	abc
P648,05(CRAW 50)	11.06	abc
PBI 1908-49-7	9.99	cdefgh
P693,02	9.65	efghij
PBI 1013-13-3	9.70	defghi
3431-01	10.54	bcdef
3458-34	9.75	defhi
3494-01	10.72	bcdef
88PBI9	10.78	abcde
CRAW 45	11.96	a
PBI 1641-25	10.77	bcde
3415-20	10.36	bcdefg
Konini	10.43	bcdefg
3496-03	9.73	defhi
3665-30	11.24	ab
3665-08	10.89	abcd
Otane	8.35	k
CR5/188(PSW 251)	9.43	ghijk
CRSW 6(PSW 251	10.37	bcdefg
CRSW 18	9.88	cdefgh
CRSW 19	8.45	j
CRSW 22	9.57	efhijk
Genero 81	9.64	efghij
18-IBSWN-136	8.94	hijk
P694,03	9.50	fghijk
Oroua	9.45	ghijk
Karamu	9.67	efghij
Rongotea	9.66	efghij
Otane rogue	9.67	efghij
Transvaal	9.45	ghijk
S.F.A 1116	8.92	hijk
659/16	9.10	hhijk
449,02/22	8.56	ijk
441,021	9.90	cdefgh
722,02	10.52	bcdefg
Se	0.61	

Means with same letter are not significantly different at 5% level.

Table 4.14 Continued **(Number of fertile tillers and total tillers)**

Genotypes	FTN Mean(no.)	Sig. group	TN Mean(no.)	Sig. group
Avalon	N.F.		N.F.	
C3640	N.F.		N.F.	
CR3/135	N.F.		N.F.	
CR3/136	N.F.		N.F.	
3410-10	N.F.		N.F.	
3413-09	N.F.		N.F.	
Batten	5.06	fghijk	7.85	ghijkl
C7205 (CRAW 17	5.53	defghghi	10.41	bcde
PBI 1908-49-5	7.27	a	12.60	A
P648,05(CRAW 50)	6.72	abcd	11.05	abc
PBI 1908-49-7	6.10	abcdefg	10.45	bcd
P693,02	5.85	bcdefghi	9.72	bcdef
PBI 1013-13-3	5.48	defghij	8.40	fghijk
3431-01	5.82	bcdefghi	11.12	ab
3458-34	5.72	cdefghi	8.77	defghi
3494-01	6.47	abcde	9.02	defghi
88PBI9	4.98	ghijk	9.23	cdefg
CRAW 45	3.93	k	12.73	a
PBI 1641-25	4.60	ijk	9.07	defghi
3415-20	4.90	ghijk	8.25	fghijk
Konini	6.43	abcde	9.70	bcdefg
3496-03	5.57	cdefghij	9.22	dcefg
3665-30	6.00	abcdefgh	11.00	abc
3665-08	7.01	ab	10.28	bcde
Otane	4.80	hijk	6.22	lm
CR5/188(PSW 251)	4.75	hijk	6.57	klm
CRSW 6(PSW 251	6.15	abcdefg	9.57	bcdefg
CRSW 18	6.32	abcdef	9.12	defgh
CRSW 19	4.35	jk	5.65	m
CRSW 22	6.70	abcd	8.95	defghi
Genero 81	4.95	ghijk	6.73	jklm
18-IBSWN-136	5.11	fghijk	8.58	efghij
P694,03	5.45	defghij	7.27	hijklm
Oroua	6.50	abcde	8.75	defghi
Karamu	6.65	abcd	8.12	fghijk
Rongotea	5.91	bcdefgh	8.25	fghijk
Otane rogue	6.00	abcdefgh	8.07	fghijkl
Transvaal	5.93	bcdefgh	7.95	fghijkl
S.F.A 1116	6.57	abcd	8.14	fhgijk
659/16	5.27	efghij	7.23	ijklm
449,02/22	7.02	ab	9.45	bcdefg
441,021	6.83	abc	9.02	defghi
722,02	6.85	abc	9.80	bcdef
Se	0.64		0.94	

Means with same letter are not significantly different at 5% level.

Table 4.14 Continued **(Fertility ratio of tillers and Internod number)**

Genotypes	FRAT Mean(ratio)	Sig. group	INTN Mean(no.)	Sig. group
Avalon	N.F.		N.F.	
C3640	N.F.		N.F.	
CR3/135	N.F.		N.F.	
CR3/136	N.F.		N.F.	
3410-10	N.F.		N.F.	
3413-09	N.F.		N.F.	
Batten	0.662	cdefghij	4.94	lm
C7205 (CRAW 17)	0.528	lm	5.05	ijklm
PBI 1908-49-5	0.595	ijklm	5.05	ijklm
P648,05(CRAW 50)	0.610	ghijklm	5.00	klm
PBI 1908-49-7	0.584	jklm	5.02	jklm
P693,02	0.600	hijklm	5.47	bcdef
PBI 1013-13-3	0.653	cdefghij	4.81	m
3431-01	0.526	lm	5.32	cdefghij
3458-34	0.664	cdefghij	5.35	cdefghij
3494-01	0.729	abcdefg	5.77	ab
88PBI9	0.556	klm	5.20	efghijkl
CRAW 45	0.327	n	5.47	bcdef
PBI 1641-25	0.511	m	5.10	ghijklm
3415-20	0.622	efghijkl	5.95	a
Konini	0.666	cdefghij	5.43	bcdefgh
3496-03	0.618	fghijklm	5.10	ghijklm
3665-30	0.549	klm	5.32	cdefghij
3665-08	0.683	cdefghij	5.30	cdefghij
Otane	0.764	abc	5.40	cdefghi
CR5/188(PSW 251)	0.739	abcde	5.55	bcde
CRSW 6(PSW 251	0.643	cdefghij	5.52	bcde
CRSW 18	0.699	bcdefghi	5.22	defghijk
CRSW 19	0.758	abcd	5.50	bcde
CRSW 22	0.746	abcd	5.55	bcde
Genero 81	0.760	abcd	5.41	bcdefghi
18-IBSWN-136	0.643	defghijk	5.12	fghijklm
P694,03	0.746	abcd	5.27	cdefghij
Oroua	0.736	abcdef	5.25	defghijk
Karamu	0.817	ab	5.06	hijklm
Rongotea	0.718	abcdefgh	5.36	cdefghij
Otane rogue	0.762	cd	5.40	cdefghi
Transvaal	0.75	abcd	5.61	abc
S.F.A 1116	0.823	a	5.55	bcde
659/16	0.735	abcdef	5.45	bcdefg
449,02/22	0.733	abcdef	5.25	defghijk
441,021	0.759	abcd	5.58	bcd
722,02	0.715	abcdefgh	5.55	bcde
Se	0.061		0.185	

Means with same letter are not significantly different at 5% level.

Table 4.14 Continued **(Main stem hgight and Peduncle length)**

Genotypes	MSH Mean(mm)	Sig. group	PL Mean(mm)	Sig. group
Avalon	N.F.		N.F.	
C3640	N.F.		N.F.	
CR3/135	N.F.		N.F.	
CR3/136	N.F.		N.F.	
3410-10	N.F.		N.F.	
3413-09	N.F.		N.F.	
Batten	694	ijklmn	317	hijk
C7205 (CRAW 17	601	op	251	m
PBI 1908-49-5	681	klmn	318	hgik
P648,05(CRAW 50)	693	jklmn	324	efghi
PBI 1908-49-7	710	hijkl	330	efghi
P693,02	690	jklmn	289	kl
PBI 1013-13-3	650	mno	289	kl
3431-01	663	lmn	321	fghij
3458-34	768	defg	344	defgh
3494-01	719	ghijk	363	bcd
88PBI9	684	klmn	322	efghij
CRAW 45	560	p	212	n
PBI 1641-25	654	mno	300	ijkl
3415-20	709	hijkl	299	ijkl
Konini	802	bcde	349	cdefg
3496-03	692	jklmn	319	ghijk
3665-30	743	fghij	344	defgh
3665-08	771	bcdef	346	defgh
Otane	723	ghijk	340	defgh
CR5/188(PSW 251)	649	mno	339	defgh
CRSW 6(PSW 251)	818	bcd	347	defgh
CRSW 18	701	jikml	341	defgh
CRSW 19	743	fghij	353	cde
CRSW 22	777	bcdef	364	bcd
Genero 81	675	klmn	291	jkl
18-IBSWN-136	642	o	278	lm
P694,03	747	fghi	338	defgh
Oroua	760	efg	322	efghij
Karamu	677	klmn	352	cdef
Rongotea	769	defg	340	defgh
Otane rogue	831	b	378	bc
Transvaal	1029	a	465	a
S.F.A 1116	1077	a	475	a
659/16	824	bc	385	b
449,02/22	759	efgh	328	efghi
441,021	741	fghij	328	efghi
722,02	778	bcdef	340	defgh
Se	24		16	

Means with same letter are not significantly different at 5% level.

Table 4.14 Continued **Leaf ppearance rate (leaf/day)**
Tiller production rate (tiller/day)

Genotypes	Lar Mean(tip/d)	Sig. group	TPR Mean(til/d)	Sig. group
Avalon	0.1424	a	0.0201	efghijkl
C3640	0.1344	bcd	0.0227	bcdefghi
CR3/135	0.1157	stu	0.0257	abcdefgh
CR3/136	0.1250	fghijklmnop	0.0246	bcdefghi
3410-10	0.1276	cdefghijklm	0.0267	abcde
3413-09	0.1248	fghijklmnopq	0.0177	kl
Batten	0.1256	fghijklmnop	0.0274	abcd
C7205 (CRAW 17)	0.1209	klmnopgrst	0.0197	fghijkl
PBI 1908-49-5	0.1283	cdefghijk	0.0262	abcdef
P648,05(craw 50)	0.1280	cdefghijkl	0.0286	abc
PBI 1908-49-7	0.1221	klmnopqrst	0.0245	bcdefghi
P693,02	0.1201	mnopqrstu	0.0277	abcd
PBI 1013-13-3	0.1160	rstu	0.0182	jkl
3431-01	0.1244	ghijklmnopq	0.0192	ghijkl
3458-34	0.1228	ijklmnopqrs	0.0293	ab
3494-01	0.1321	cdef	0.0240	bcdefghi
88PBI9	0.1303	cdefgh	0.0269	abcd
CRAW 45	0.1190	pqrstu	0.0193	ghijkl
PBI 1641-25	0.1300	cdefghi	0.0190	hijkl
3415-20	0.1270	defghijklmn	0.0253	abcdefgh
Konini	0.1397	ab	0.0320	a
3496-03	0.1233	ghijklmnopqr	0.0248	bcdefghi
3665-30	0.1349	bc	0.0165	l
3665-08	0.1405	ab	0.0248	bcdefghi
Otane	0.1195	opqrstu	0.0289	ab
CR5/188(PSW 251)	0.1305	cdefg	0.0269	abcd
CRSW 6(PSW 251)	0.1290	cdefghij	0.0262	abcdef
CRSW 18	0.1266	efghijklmno	0.0258	abcdefg
CRSW 19	0.1151	tu	0.0198	fghijkl
CRSW 22	0.1196	opqrstu	0.0277	abcd
Genero 81	0.1337	bcde	0.0219	cdefghij
18-IBSWN-136	0.1296	hijklmnopqrs	0.0214	defghijk
P694,03	0.1208	lmnopqrstu	0.0273	abcd
Oroua	0.1223	jklmnopqrst	0.0248	bcdefghi
Karamu	0,1305	cdefg	0.0272	abcd
Rongotea	0.1214	klmnopqrst	0.0229	bcdefghi
Otane rogue	0.1344	bcd	0.0271	abcd
Transvaal	0.1296	cdefghij	0.0255	abcdefgh
S.F.A 1116	0.1241	hijklmnopq	0.0256	abcdefgh
659/16	0.1174	qrstu	0.0288	ab
449,02/22	0.1136	u	0.0233	bcdefghi
441,021	0.1270	defghijklmn	0.0242	bcdefghi
722,02	0.1335	bcde	0.0186	ijkl
Se	0.0091		0.0054	

Means with same letter are not significantly different at 5% level.

late flowering have usually more leaf, spikelet, and tiller numbers than early flowering genotypes (Table 4.14)

4.4.2 Environmental Means

The comparison between environmental means (Table 4.15) indicated the general effects of the environments (sowing dates) on the studied attributes, and the range of change by changing environments. Lateness of sowing caused significant reduction in the value of most of the characters. A great reduction occurred in days to flag leaf unfolding, ear emergence and anthesis by delaying sowing date from ealy winter to early summer for all genotypes except those six strong winter wheat (Table 4.15).

The change from second sowing to third and fourth sowing did not bring about significant change in characters FTN and MSH. Total tiller number was not significantly affected by sowing date. Delay in sowing date from winter (cold temperature, short days) to spring (warm temperature, long days) increased significantly LAR and TPR.

Table 4.15 Environmental means of studied characters (with LSD).

Character	ENV1	ENV2	ENV3	ENV4	Se
LFN	11.06 a	10.12 b	-	8.66 c	0.056
LAR	0.153 a	0.121 b	-	0.104 c	0.001
TPR	0.0127a	0.0179b	-	0.0422c	0.0009
DFL	119 a	103 b	63 c	47 d	0.22
DHD	136 a	119 b	77 c	59 d	0.24
DANT	141 a	123 b	80 c	64 d	0.24
SPKN	23.1 a	21.5 b	20.8 b	18.5 c	0.118
FTN	7.1 a	5.6 b	5.5 b	5.1 b	0.21
TTN	9.7 a	9.1 a	8.9 a	8.1 a	0.29
FRAT	0.76 a	0.70 b	0.64 c	0.57 d	0.015
MSH	832 a	757 b	750 b	603 c	7.80
PL	356 a	348 b	337 c	295 c	3.95
INTN	5.9 a	5.5 b	5.2 c	4.8 d	0.047

Means with same letter are not significantly different at 5% level.

Related units presented earlier (Table 3.11).

4.4.3 Genotype X Environment interaction means

The differences in response of genotypes to various environments are central in determining the vernalization and photoperiod sensitivity or the plant type of the given genotypes. The changes in genotypic means across individual environments represent the response patterns of the genotypes. These genotype X environment means for all characters (DFL, DHD, DANT, LFN, LAR, TPR, SPKN, FTN, TTN, FRAT, MSH, PL and INTN) are presented in Tables 4.16 to 4.28 respectively, and include the trends responses after examining the significance at 5% level.

Genotypes Avalon, C_3 640, CR_3/135, CR_3/136, 340-10 and 3413-09 did not flower in spring sowings and genotype CROW 45 flowered very late (only on a few tillers) in those experiments. Therefore these genotypes can be distinguished simply as a separate group. Further analysis is needed to distinguish between the remaining genotypes. Pattern of change in characters DFL, DHD and DANT were very similar and they all more or less measured the same attribute. This was first noted with the correlation results. Therefore, only one of these, DFL, were considered further in this study..

Table 4.16 The comparison of genotypic means in different environments.

Days to Flag Leaf

Genotype	ENV1	ENV2	ENV3	ENV4	Response
Avalon	134.98	122.56	N.F.	N.F.	1>2<<<3,4
C3640	130.40	116.60	N.F.	N.F.	1>2<<<3,4
CR3/135	130.85	121.27	N.F.	N.F.	1>2<<<3,4
CR3/136	132.21	122.55	N.F.	N.F.	1>2<<<3,4
3410-10	131.31	121.00	N.F.	N.F.	1>2<<<3,4
3413-09	133.85	121.74	N.F.	N.F.	1>2<<<3,4
Batten	121.80	106.23	61.50	42.59	1>2>3>4
C7205 (CRAW 17	127.23	109.30	72.00	60.52	1>2>3>4
PBI 1908-49-5-	134.25	115.01	69.00	47.15	1>2>3>4
P648,05(CRAW 50)	135.23	114.75	69.00	47.45	1>2>3>4
PBI 1908-49-7	127.90	110.25	66.50	46.05	1>2>3>4
P693,02	127.11	107.95	67.00	47.42	1>2>3>4
PBI 1013-13-3	127.78	110.50	66.50	48.49	1>2>3>4
3431-01	131.30	112.05	68.00	46.38	1>2>3>4
3458-34	120.85	105.80	63.50	44.75	1>2>3>4
3494-01	122.82	108.30	67.50	49.30	1>2>3>4
88PBI9	129.70	112.80	67.00	49.30	1>2>3>4
CRAW 45	134.08	118.20	81.00	67.20	1>2>3>4
PBI 1641-25	134.63	112.35	69.50	47.53	1>2>3>4
3415-20	130.75	110.90	65.00	45.94	1>2>3>4
Konini	122.20	104.75	65.00	50.54	1>2>3>4
3496-03	124.80	107.08	68.50	48.00	1>2>3>4
3665-30	126.97	108.10	69.00	54.33	1>2>3>4
3665-08	119.35	105.40	65.00	49.44	1>2>3>4
Otane	103.40	92.15	55.00	42.07	1>2>3>4
CR5/188(PSW 251)	102.65	89.40	57.00	43.25	1>2>3>4
CRSW 6(PSW 251	119.45	105.15	62.50	44.75	1>2>3>4
CRSW 18	118.24	101.10	59.00	42.30	1>2>3>4
CRSW 19	104.65	91.70	55.50	41.65	1>2>3>4
CRSW 22	119.65	104.00	60.00	43.35	1>2>3>4
Genero 81	100.94	91.30	55.50	51.50	1>2>3\\4
18-IBSWN-136	103.00	90.62	54.00	50.11	1>2>3\\4
P694,03	118.25	98.40	57.00	41.00	1>2>3>4
Oroua	116.30	100.70	56.50	40.30	1>2>3>4
Karamu	105.40	93.05	57.50	42.25	1>2>3>4
Rongotea	119.53	103.46	62.00	43.25	1>2>3>4
Otane Rogue	100.25	90.60	59.00	50.01	1>2>3>4
Transvaal	106.80	93.25	56.00	43.03	1>2>3>4
S. F.a 1116	105.75	91.45	56.50	42.40	1>2>3>4
659/16	117.00	96.22	57.00	40.70	1>2>3>4
449,02/22	108.15	95.70	59.00	45.66	1>2>3>4
441,021	117.99	102.10	61.50	42.55	1>2>3>4
722,02	120.11	106.59	65.00	47.98	1>2>3>4

N.F., Not Flowered

<<<, Spring Sowing are extremely greater then winter sowing in true winter types.

>, significantly decreased \\, non significantly decreased

<, significantly increased //, non significantly increased

Table 4.17 The comparison of genotypic means in different environments.

Days to Heading

Genotype	ENV1	ENV2	ENV3	ENV4
Avalon	152.54	139.56	N.F.	N.F.
C3640	145.70	131.85	N.F.	N.F.
CR3/135	149.55	138.06	N.F.	N.F.
CR3/136	149.98	138.99	N.F.	N.F.
3410-10	150.45	138.85	N.F.	N.F.
3413-09	153.08	139.93	N.F.	N.F.
Batten	140.10	121.02	77.50	54.09
C7205 (CRAW 17	145.14	126.07	84.50	70.95
PBI 1908-49-5	148.75	130.19	82.50	61.36
P648,05(CRAW 50)	149.93	129.55	82.50	63.72
PBI 1908-49-7	145.14	126.00	82.00	63.49
P693,02	143.90	124.90	82.00	63.06
PBI 1013-13-3	145.34	126.60	81.50	63.60
3431-01	147.70	127.40	83.00	61.91
3458-34	138.70	120.55	75.50	58.65
3494-01	139.39	121.25	80.00	63.72
88PBI9	146.45	128.95	82.00	65.28
CRAW 45	149.27	134.55	95.00	79.28
PBI 1641-25	150.79	128.00	85.50	64.94
3415-20	148.55	127.00	81.00	61.94
Konini	140.05	119.35	79.00	63.11
3496-03	141.40	121.25	81.00	62.91
3665-30	143.81	123.15	83.50	65.38
3665-08	137.85	120.55	79.50	64.77
Otane	119.55	108.85	68.50	52.61
CR5/188(PSW 251)	118.30	105.85	70.00	56.80
CRSW 6(PSW 251	135.75	117.80	75.50	56.25
CRSW 18	135.48	115.15	72.50	52.55
CRSW 19	120.35	108.50	69.00	52.65
CRSW 22	137.80	119.75	73.00	54.40
Genero 81	118.42	107.45	69.50	60.66
18-IBSWN-136	118.62	107.57	67.00	62.83
P694,03	135.80	113.50	72.00	51.55
Oroua	132.95	115.60	69.00	49.85
Karamu	119.80	108.25	69.00	52.85
Rongotea	137.68	118.82	76.00	56.20
Otane Rogue	116.90	106.45	72.50	60.23
Transvaal	122.77	109.55	69.00	52.60
S. F.a 1116	121.85	107.90	69.00	52.25
659/16	134.65	113.36	71.00	50.70
449,02/22	123.35	111.75	71.50	57.16
441,021	136.00	118.47	75.00	53.30
722,02	137.68	120.58	78.00	61.01

Table 4.18 The comparison of genotypic means in different environments.
Days to Anthesis

Genotype	ENV1	ENV2	ENV3	ENV4
Avalon	155.17	141.85	N.F	N.F.
C3640	149.70	135.15	N.F	N.F.
CR3/135	152.20	139.22	N.F	N.F.
CR3/136	152.60	140.27	N.F	N.F.
3410-10	153.18	141.27	N.F	N.F.
3413-09	155.75	140.92	N.F	N.F.
Batten	143.30	124.68	80.00	59.37
C7205 (CRAW 17	147.87	128.27	88.00	75.86
PBI 1908-49-5	152.60	133.85	86.50	65.76
P648,05(CRAW 50)	153.71	133.15	85.50	68.00
PBI 1908-49-7	149.04	129.35	85.00	67.45
P693,02	147.84	128.60	84.50	66.61
PBI 1013-13-3	149.11	129.40	85.00	68.66
3431-01	151.70	131.05	86.00	66.73
3458-34	142.90	124.70	79.00	63.50
3494-01	144.78	127.00	82.00	67.38
88PBI9	149.90	131.55	84.50	69.29
CRAW 45	151.69	136.70	99.00	83.50
PBI 1641-25	154.77	131.40	88.00	68.79
3415-20	151.50	129.60	84.50	65.55
Konini	144.65	124.50	82.00	67.00
3496-03	146.35	125.21	84.00	66.84
3665-30	147.95	126.65	85.00	68.22
3665-08	143.40	124.60	82.00	68.32
Otane	124.80	112.85	71.50	57.88
CR5/188(PSW 251)	124.65	111.50	72.50	61.65
CRSW 6(PSW 251	141.75	123.30	79.50	61.60
CRSW 18	140.20	119.95	75.50	57.60
CRSW 19	127.10	113.05	72.00	56.65
CRSW 22	142.60	124.05	76.50	59.07
Genero 81	122.67	111.75	73.00	66.50
18-IBSWN-136	124.40	112.06	71.50	65.81
P694,03	141.20	118.60	74.00	56.25
Oroua	137.27	119.50	73.00	55.45
Karamu	126.25	112.10	71.50	57.70
Rongotea	143.07	122.65	79.50	61.12
Otane Rogue	123.15	112.50	76.00	65.93
Transvaal	131.22	115.93	74.00	57.72
S.F.A 1116	129.45	114.75	74.00	58.70
659/16	138.20	118.18	74.00	56.30
449,02/22	130.75	114.50	76.00	62.60
441,021	141.57	121.10	78.50	58.60
722,02	142.98	124.89	81.50	66.21

Table 4.19 The comparison of genotypic means in different environments.
The Number of Leaves

Genotype	ENV1	ENV2	ENV4	Response
Avalon	14.18	14.62	N.F.	1,2<<<4
C3640	13.20	13.15	N.F	1,2<<<4
CR3/135	11.30	12.32	N.F	1,2<<<4
CR3/136	12.81	13.66	N.F	1,2<<<4
3410-10	12.33	13.32	N.F	1,2<<<4
3413-09	13.10	13.28	N.F	1,2<<<4
Batten	12.05	10.37	7.94	1>2>3
C7205 (CRAW 17	12.42	11.45	9.90	1>2>3
PBI 1908-49-5	12.80	11.53	8.94	1>2>3
P648,05(CRAW 50)	12.99	11.20	9.00	1>2>3
PBI 1908-49-7	11.32	10.35	8.31	1>2>3
P693,02	10.89	10.05	8.00	1>2>3
PBI 1013-13-3	11.00	10.00	8.11	1>2>3
3431-01	12.15	10.65	8.83	1>2>3
3458-34	11.20	10.25	7.80	1>2>3
3494-01	11.88	10.80	9.47	1>2>3
88PBI9	12.10	11.00	9.25	1>2>3
CRAW 45	12.20	11.72	_	1>2>-
PBI 1641-25	12.53	10.95	8.82	1>2>3
3415-20	11.90	10.45	8.73	1>2>3
Konini	11.35	10.20	9.73	1>2\\3
3496-03	11.45	9.73	8.00	1>2>3
3665-30	12.43	11.35	9.94	1>2>3
3665-08	11.85	10.95	9.88	1>2>3
Otane	8.90	8.30	8.07	1>2\\3
CR5/188(PSW 251)	9.95	9.40	8.95	1>2>3
CRSW 6(PSW 251	11.95	10.70	8.45	1>2>3
CRSW 18	11.60	10.15	7.90	1>2>3
CRSW 19	8.90	8.60	7.85	1\\2>3
CRSW 22	11.20	9.65	7.85	1>2>3
Genero 81	8.85	9.65	10.41	1<2<3
18-IBSWN-136	8.70	8.90	8.94	1//2//3
P694,03	11.25	9.94	7.30	1>2>3
Oroua	11.01	9.80	7.55	1>2>3
Karamu	10.30	9.90	8.80	1\\2>3
Rongotea	11.00	9.94	8.05	1>2>3
Otane Rogue	9.00	9.50	10.41	1<2<3
Transvaal	9.90	9.55	8.90	1\\2>3
S. F.a 1116	9.25	8.80	8.75	1>2\\3
659/16	10.80	9.10	7.40	1>2>3
449,02/22	9.00	8.85	7.82	1\\2>3
441,021	11.26	9.85	8.60	1>2>3
722,02	11.73	10.73	9.09	1>2>3

N.F., Not Flowered
<<<, Spring sowings are extremely greater than winter sowings in true winter types.
>, significantly decreased \\, non significantly decreased
<, significantly increased //, non significantly increased

Table 4.20 The comparison of genotypic means in different environments.
Leaf Appearance Rate

Genotype	ENV1	ENV2	ENV4	Response
Avalon	0.1168	0.1479	0.1622	1<2<4
C3640	0.1102	0.1392	0.1537	1<2<4
CR3/135	0.0949	0.1205	0.1316	1<2//4
CR3/136	0.1071	0.1347	0.1331	1<2//4
3410-10	0.1053	0.1353	0.1419	1<2//4
3413-09	0.1088	0.1358	1.8367	1<2//4
Batten	0.1128	0.1159	0.1481	1//2<4
C7205 (CRAW 17	0.1076	0.1265	0.1285	1<2\\4
PBI 1908-49-5	0.1040	0.1154	0.1654	1//2<4
P648,05(CRAW 50)	0.1054	0.1129	0.1657	1//2<4
PBI 1908-49-7	0.0959	0.1117	0.1588	1//2<4
P693,02	0.0949	0.1144	0.1510	1<2<4
PBI 1013-13-3	0.0935	0.1098	0.1448	1<2<4
3431-01	0.0989	0.1088	0.1653	1//2<4
3458-34	0.1070	0.1162	0.1449	1//2<4
3494-01	0.1074	0.1191	0.1698	1//2<4
88PBI9	0.1061	0.1164	0.1681	1//2<4
CRAW 45	0.1009	0.1227	0.1334	1<2//4
PBI 1641-25	0.1061	0.1175	0.1664	1//2<4
3415-20	0.1032	0.1166	0.1611	1<2<4
Konini	0.1141	0.1233	0.1815	1//2<4
3496-03	0.1066	0.1114	0.1518	1//2<4
3665-30	0.1183	0.1265	0.1599	1//2<4
3665-08	0.1147	0.1272	0.1794	1//2<4
Otane	0.0925	0.1120	0.1539	1<2<4
CR5/188(PSW 251)	0.0974	0.1288	0.1654	1<2<4
CRSW 6(PSW 251	0.1126	0.1196	0.1548	1//2<4
CRSW 18	0.1105	0.1215	0.1479	1//2<4
CRSW 19	0.0920	0.1174	0.1356	1<2<4
CRSW 22	0.1084	0.1117	0.1387	1//2<4
Genero 81	0.0918	0.1321	0.1771	1<2<4
18-IBSWN-136	0.0986	0.1152	0.1550	1<2<4
P694,03	0.1140	0.1198	0.1285	1//2//4
Oroua	0.1112	0.1150	0.1407	1//2<4
Karamu	0.1083	0.1307	0.1524	1<2<4
Rongotea	0.1059	0.1116	0.1466	1//2<4
Otane Rogue	0.0848	0.1284	0.1898	1<2<4
Transvaal	0.0932	0.1265	0.1690	1<2<4
S.F.A 1116	0.0958	0.1183	0.1580	1<2<4
659/16	0.1091	0.1151	0.1279	1//2<4
449,02/22	0.0861	0.1129	0.1417	1<2<4
441,021	0.1068	0.1150	0.1592	1//2<4
722,02	0.1191	0.1243	0.1572	1//2<4

N.F., Not Flowered
>, significantly decreased
<, significantly increased
\\ non significantly decreased
// non significantly increased

Table 4.21 The comparison of genotypic means in different environments.
Tiller Production Rate

Genotype	ENV1	ENV2	ENV4	Response
Avalon	0.0077	0.0228	0.0254	1<2//4
C3640	0.0063	0.0152	0.0316	1//2<4
CR3/135	0.0073	0.0181	0.0293	1//2<4
CR3/136	0.0077	0.0173	0.0326	1//2<4
3410-10	0.0057	0.0216	0.0306	1<2//4
3413-09	0.0091	0.0194	0.0286	1//2<4
Batten	0.0025	0.0142	0.0435	1//2<4
C7205 (CRAW 17	0.0115	0.0197	0.0370	1//2<4
PBI 1908-49-5	0.0110	0.0195	0.0468	1//2<4
P648,05(CRAW 50)	0.0083	0.0198	0.0455	1//2<4
PBI 1908-49-7	0.0089	0.0207	0.0507	1//2<4
P693,02	0.0152	0.0243	0.0427	1//2//4
PBI 1013-13-3	0.0032	0.0158	0.0401	1//2<4
3431-01	0.0143	0.0198	0.0445	1//2<4
3458-34	0.0142	0.0187	0.0529	1//2<4
3494-01	0.0071	0.0189	0.0475	1//2<4
88PBI9	0.0151	0.0170	0.0509	1//2<4
CRAW 45	0.0134	0.0220	0.0525	1//2<4
PBI 1641-25	0.0109	0.0213	0.0397	1//2<4
3415-20	0.0179	0.0180	0.0449	1//2<4
Konini	0.0140	0.0192	0.0426	1<2//4
3496-03	0.0112	0.0199	0.0432	1//2<4
3665-30	0.0137	0.0176	0.0183	1//2//<4
3665-08	0.0079	0.0186	0.0479	1//2<4
Otane	0.0188	0.0240	0.0441	1//2//4
CR5/188(PSW 251)	0.0152	0.0153	0.0502	1//2<4
CRSW 6(PSW 251	0.0128	0.0146	0.0511	1//2<4
CRSW 18	0.0046	0.0209	0.0520	1//2<4
CRSW 19	0.0165	0.0128	0.0303	1//2//4
CRSW 22	0.0091	0.0161	0.0581	1//2<4
Genero 81	0.0253	0.0175	0.0230	1//2//4
18-IBSWN-136	0.0371	0.0159	0.0429	1<2<4
P694,03	0.0124	0.0129	0.0389	1//2<4
Oroua	0.0151	0.0138	0.0529	1//2<4
Karamu	0.0207	0.0169	0.0369	1//2<4
Rongotea	0.0145	0.0166	0.0504	1//2<4
Otane Rogue	0.0128	0.0162	0.0398	1//2<4
Transvaal	0.0212	0.0121	0.0479	1//2<4
S.F.A 1116	0.0189	0.0173	0.0403	1//2<4
659/16	0.0135	0.0174	0.0457	1//2<4
449,02/22	0.0162	0.0175	0.0528	1//2<4
441,021	0.0051	0.0165	0.0484	1//2<4
722,02	0.0129	0.0188	0.0410	1//2<4

N.F., Not Flowered
>, significantly decreased
<, significantly increased
\\, non significantly decreased
//, non significantly increased

Table 4.22 The comparison of genotypic means in different environments.

Spikelet Number

Genotype	ENV1	ENV2	ENV3	ENV4	Response
Avalon	23.96	24.40	N.F.	N.F.	-
C3640	23.50	22.90	N.F.	N.F.	-
CR3/135	24.15	21.92	N.F.	N.F.	-
CR3/136	24.87	24.05	N.F.	N.F.	-
3410-10	24.54	26.15	N.F.	N.F.	-
3413-09	25.15	25.59	N.F.	N.F.	-
Batten	23.15	20.39	18.90	16.04	1>2>3>4
C7205 (CRAW 17	24.20	22.45	21.10	20.65	1>2>3\\4
PBI 1908-49-5	26.10	27.05	24.20	19.58	1//2>3>4
P648,05(CRAW 50)	25.86	26.10	23.80	19.85	1//2>3>4
PBI 1908-49-7	25.81	23.70	23.40	19.35	1>2\\3>4
P693,02	23.39	22.50	19.00	18.75	1>\\>3\\4
PBI 1013-13-3	26.40	25.00	23.10	20.68	1>2>3>4
3431-01	24.20	23.85	22.70	18.70	1\\2\\3>4
3458-34	23.10	21.35	21.20	17.75	1>2\\3>4
3494-01	26.00	23.00	21.90	20.75	1>2\\3\\4
88PBI9	23.92	21.45	20.90	19.80	1>2\\3\\4
CRAW 45	23.93	23.31	23.90	20.20	1\\2//3>4
PBI 1641-25	25.87	26.55	24.30	20.96	1\\2>3>4
3415-20	23.60	22.60	21.40	19.05	1\\2>3>4
Konini	19.50	17.85	19.00	16.82	1>2//3>4
3496-03	21.50	19.80	20.70	18.80	1>2//3>4
3665-30	20.47	20.50	20.30	16.45	1//2\\3>4
3665-08	24.40	21.45	21.40	19.30	1>2\\3>4
Otane	19.85	19.20	19.80	17.83	1\\2//3>4
CR5/188(PSW 251)	21.30	19.90	20.20	18.50	1>2//3>4
CRSW 6(PSW 251	24.55	22.40	21.90	17.80	1>2\\3>4
CRSW 18	24.35	20.65	18.70	16.65	1>2>3>4
CRSW 19	21.82	20.55	21.00	19.00	1>2//3>4
CRSW 22	23.55	20.40	18.80	17.00	1>2>3>4
Genero 81	19.52	20.20	20.30	19.65	1//2//3\\4
18-IBSWN-136	20.05	19.57	19.77	18.88	1\\2//3\\4
P694,03	23.75	21.50	20.20	17.90	1>2>3>4
Oroua	22.43	19.20	18.00	14.90	1>2>3>4
Karamu	22.10	19.75	19.00	17.40	1>2\\3>4
Rongotea	22.92	20.00	19.40	16.60	1>2\\3>4
Otane Rogue	18.10	18.15	19.70	18.40	1//2<3>4
Transvaal	23.14	21.00	20.30	19.21	1>2\\3>4
S. F.a 1116	22.35	19.80	19.70	19.45	1>2\\3>4
659/16	25.20	22.00	20.70	17.97	1>2>3>4
449,02/22	22.50	20.45	20.60	18.35	1>2//3>4
441,021	23.98	20.85	20.10	17.15	1>2>\\>4
722,02	22.63	20.13	20.10	18.94	1>2\\3\\4

N.F., Not Flowered
>, significantly decreased
<, significantly increased
\\, non significantly decreased
//, non significantly increased

Table 4.23 The comparison of genotypic means in different environments.

The Number of Fertile Tillers

Genotype	ENV1	ENV2	ENV3	ENV4
Avalon	6.20	8.50	0.00	0.00
C3640	5.70	5.30	0.00	0.00
CR3/135	6.60	3.50	0.00	0.00
CR3/136	8.20	5.30	0.00	0.00
3410-10	4.90	5.90	0.00	0.00
3413-09	8.50	5.90	0.00	0.00
Batten	5.60	4.80	5.80	4.05
C7205 (CRAW 17	8.50	5.80	4.40	3.45
PBI 1908-49-5	6.50	7.80	7.60	7.20
P648,05(CRAW 50)	7.50	7.00	7.20	5.20
PBI 1908-49-7	8.20	4.10	5.80	6.30
P693,02	7.30	6.00	4.70	5.40
PBI 1013-13-3	5.40	5.60	5.90	5.05
3431-01	6.70	5.30	6.20	5.10
3458-34	6.90	6.10	4.90	5.00
3494-01	8.10	5.40	5.00	7.40
88PBI9	6.02	4.40	4.40	5.10
CRAW 45	5.30	4.20	3.80	2.45
PBI 1641-25	4.50	5.60	4.00	4.30
3415-20	6.10	4.40	5.50	3.60
Konini	9.10	5.40	5.70	5.55
3496-03	6.30	5.00	6.30	4.70
3665-30	6.80	4.90	6.70	5.60
3665-08	8.30	6.75	6.50	6.50
Otane	6.30	4.80	4.70	3.40
CR5/188(PSW 251)	5.40	4.70	4.80	4.10
CRSW 6(PSW 251	6.60	6.80	6.00	5.20
CRSW 18	8.30	6.70	5.60	4.70
CRSW 19	6.30	4.30	3.80	3.00
CRSW 22	9.40	5.70	5.90	5.80
Genero 81	5.00	5.90	4.90	4.00
18-IBSWN-136	7.70	4.15	4.70	3.90
P694,03	7.40	5.50	4.70	4.20
Oroua	8.10	5.10	7.00	5.80
Karamu	8.70	6.60	5.00	6.30
Rongotea	7.37	4.07	6.00	6.20
Otane rogue	4.70	6.10	6.10	7.10
Transvaal	7.72	5.40	5.80	4.80
S. F.A 1116	8.10	6.30	6.10	5.80
659/16	7.17	5.05	4.90	3.97
449,02/22	10.20	6.30	6.70	4.90
41,021	8.72	6.20	5.60	6.80
722,02	6.40	6.50	7.50	7.00

Table 4.24 The comparison of genotypic means in different environments.

The Number of Total Tillers

Genotype	ENV1	ENV2	ENV3	ENV4
Avalon	10.50	16.30	-	-
C3640	9.70	10.20	-	-
CR3/135	8.70	11.20	-	-
CR3/136	10.50	12.70	-	-
3410-10	6.40	13.50	-	-
3413-09	13.00	11.70	-	-
Batten	6.90	7.60	8.30	8.60
C7205 (CRAW 17	11.20	9.90	9.70	10.85
PBI 1908-49-5	14.30	12.20	12.00	11.90
P648,05(CRAW 50)	12.60	11.50	11.10	9.00
PBI 1908-49-7	11.70	8.60	11.60	9.90
P693,02	12.10	9.60	8.60	8.60
PBI 1013-13-3	8.00	8.30	8.50	8.80
3431-01	13.30	9.40	12.40	9.40
3458-34	10.20	8.90	7.60	8.40
3494-01	8.50	7.50	7.90	12.20
88PBI9	11.92	8.30	6.90	9.80
CRAW 45	11.27	11.20	13.20	15.27
PBI 1641-25	9.90	9.30	7.90	9.20
3415-20	11.00	6.30	8.40	7.30
Konini	13.00	7.40	9.40	9.00
3496-03	9.60	7.30	11.10	8.90
3665-30	13.40	9.70	12.00	8.90
3665-08	10.90	9.32	10.00	10.90
Otane	7.20	6.10	6.20	5.40
CR5/188(PSW 251)	5.70	5.80	6.80	8.00
CRSW 6(PSW 251	9.80	9.70	9.20	9.60
CRSW 18	10.90	9.70	7.40	8.50
CRSW 19	6.80	5.20	5.80	4.80
CRSW 22	10.60	7.80	8.90	8.50
Genero 81	5.12	7.00	8.10	6.70
18-IBSWN-136	8.20	5.52	9.60	11.00
P694,03	9.50	6.90	6.60	6.10
Oroua	10.10	7.00	9.00	8.90
Karamu	9.50	7.50	6.50	9.00
Rongotea	8.45	6.05	8.60	9.90
Otane Rogue	5.60	7.30	8.90	10.50
Transvaal	8.50	6.60	9.30	7.40
S. F.a 1116	8.40	6.50	8.27	9.40
659/16	7.72	6.57	6.40	8.22
449,02/22	11.00	8.00	9.70	9.10
441,021	9.90	8.30	7.90	10.00
722,02	7.60	9.30	11.70	10.60

Table 4.25 The comparison of genotypic means in different environments. **Fertility Ratio of Tillers**

Genotype	ENV1	ENV2	ENV4	ENV4	Response
Avalon	0.587	0.521	n.f.	n.f.	1\\2>>>3,4
C3640	0.587	0.525	n.f.	n.f.	1\\2>>>3,4
CR3/135	0.761	0.314	n.f.	n.f.	1>2>>>3,4
CR3/136	0.773	0.416	n.f.	n.f.	1>2>>>3,4
3410-10	0.757	0.432	n.f.	n.f.	1>2>>>3,4
3413-09	0.647	0.506	n.f.	n.f.	1\\2>>>3,4
Batten	0.815	0.637	0.696	0.497	1>2//3>4
C7205 (CRAW 17)	0.749	0.584	0.452	0.324	1>2\\3\\4
PBI 1908-49-5	0.451	0.636	0.682	0.609	1<2\\3\\4
P648,05(CRAW 50)	0.592	0.608	0.658	0.580	1//2//3\\4
PBI 1908-49-7	0.688	0.476	0.535	0.637	1>2//3//4
P693,02	0.604	0.619	0.547	0.628	1//2\\3//4
PBI 1013-13-3	0.670	0.668	0.690	0.580	1\\2//3\\4
3431-01	0.498	0.563	0.501	0.540	1//2\\3//4
3458-34	0.698	0.700	0.663	0.595	1//2\\3\\4
3494-01	0.945	0.726	0.632	0.609	1>2\\3\\4
88PBI9	0.507	0.528	0.638	0.550	1//2//3\\4
CRAW 45	0.469	0.370	0.290	0.176	1\\2\\3\\4
PBI 1641-25	0.470	0.601	0.505	0.467	1//2\\3\\4
3415-20	0.568	0.702	0.726	0.493	1//2//3>4
Konini	0.697	0.729	0.613	0.625	1//2\\3//4
3496-03	0.661	0.682	0.582	0.544	1//2\\3\\4
3665-30	0.503	0.504	0.555	0.632	1//2//3//4
3665-08	0.761	0.723	0.650	0.595	1\\2\\3\\4
Otane	0.878	0.779	0.754	0.644	1\\2\\3\\4
CR5/188(PSW 251)	0.948	0.810	0.699	0.500	1\\2\\3>4
CRSW 6(PSW 251	0.679	0.708	0.651	0.534	1//2\\3\\4
CRSW 18	0.788	0.691	0.755	0.559	1//2\\3>4
CRSW 19	0.927	0.818	0.652	0.635	1\\2>3\\4
CRSW 22	0.888	0.731	0.682	0.682	1>2>3//4
Genero 81	0.975	0.845	0.624	0.598	1\\2>3\\4
18-IBSWN-136	0.937	0.755	0.509	0.371	1>2>3\\4
P694,03	0.790	0.795	0.713	0.684	1//2\\3\\4
Oroua	0.793	0.726	0.776	0.646	1\\2//3\\4
Karamu	0.916	0.880	0.762	0.708	1\\2\\3\\4
Rongotea	0.872	0.681	0.695	0.624	1>2//3\\4
Otane rogue	0.850	0.835	0.685	0.677	1\\2\\3//4
Transvaal	0.906	0.818	0.621	0.659	1\\2>3//4
S.F.A 1116	0.964	0.965	0.740	0.621	1//2>3\\4
659/16	0.928	0.766	0.765	0.483	1>2\\3\\4
449,02/22	0.916	0.787	0.685	0.545	1\\2\\3\\4
441,021	0.880	0.748	0.706	0.701	1\\2\\3\\4
722,02	0.835	0.695	0.667	0.660	1\\2\\3\\4

N.F., Not Flowered
>>>, Spring sowing are extremely lower than winter sowing in true winter types
>, significantly decreased \\, non significantly decreased
<, significantly increased //, non significantly increased

Table 4.26 The comparison of genotypicmeans in different environments.

Main Stem Height

Genotype	ENV1	ENV2	ENV3	ENV4
Avalon	668	560	NF	NF
C3640	777	655	NF	NF
CR3/135	720	530	NF	NF
CR3/136	624	607	NF	NF
3410-10	622	633	NF	NF
3413-09	729	663	NF	NF
Batten	787	707	700	583
C7205 (CRAW 17	669	607	614	513
PBI 1908-49-5	783	677	697	566
P648,05(CRAW 50)	814	717	677	565
PBI 1908-49-7	811	662	739	629
P693,02	785	712	680	585
PBI 1013-13-3	726	675	685	517
3431-01	732	683	662	577
3458-34	883	783	843	564
3494-01	803	730	714	631
88PBI9	797	659	684	595
CRAW 45	688	611	558	383
PBI 1641-25	737	710	632	536
3415-20	795	759	713	571
Konini	905	800	796	709
3496-03	775	670	695	629
3665-30	851	753	739	631
+3665-08	871	757	795	661
Otane	845	777	719	550
CR5/188(PSW 251)	707	627	741	526
CRSW 6(PSW 251	875	850	901	646
CRSW 18	839	706	736	526
CRSW 19	842	811	735	585
CRSW 22	885	797	783	644
Genero 81	686	744	747	525
18-IBSWN-136	735	651	620	560
P694,03	824	825	769	572
Oroua	916	722	788	614
Karamu	765	713	658	574
Rongotea	881	785	803	608
Otane Rogue	903	861	886	673
Transvaal	1174	1010	1066	866
S. F.a 1116	1202	1132	1098	876
659/16	965	822	874	637
449,02/22	862	761	827	588
441,021	853	685	826	603
722,02	809	813	815	675

Table 4.27 The comparison of genotypic means in different environments.

Peduncle Length

Genotype	ENV1	ENV2	ENV3	ENV4
Avalon	273	255	N.F.	N.F.
C3640	275	261	N.F.	N.F.
CR3/135	323	267	N.F.	N.F.
CR3/136	268	264	N.F.	N.F.
3410-10	292	265	N.F.	N.F.
3413-09	316	264	N.F.	N.F.
Batten	322	309	334	303
C7205 (CRAW 17	293	266	256	190
PBI 1908-49-5	330	327	324	290
P648,05(CRAW 50)	360	329	311	298
PBI 1908-49-7	350	310	349	310
P693,02	307	281	302	264
PBI 1013-13-3	295	298	306	257
3431-01	337	319	328	299
3458-34	359	325	395	299
3494-01	370	368	371	343
88PBI9	344	307	340	299
CRAW 45	254	265	227	103
PBI 1641-25	322	320	291	270
3415-20	288	317	308	282
Konini	398	373	329	297
3496-03	336	306	320	314
3665-30	385	344	333	313
3665-08	385	349	340	309
Otane	368	341	368	282
CR5/188(PSW 251)	373	332	365	285
CRSW 6(PSW 251	343	360	370	315
CRSW 18	349	328	377	311
CRSW 19	381	369	370	293
CRSW 22	365	366	380	347
Genero 81	325	304	308	229
18-IBSWN-136	311	286	266	249
P694,03	342	354	349	309
Oroua	358	295	328	308
Karamu	370	359	359	320
Rongotea	335	350	365	311
Otane Rogue	425	387	385	316
Transvaal	545	412	505	401
S. F.a 1116	499	518	492	394
659/16	380	391	431	336
449,02/22	387	310	361	255
441,021	326	327	365	293
722,02	346	347	354	314

Table 4.28 The comparison of genotypic means in different environments.

The Number of Internods

Genotype	ENV1	ENV2	ENV3	ENV4
Avalon	5.70	5.00	-	-
C3640	6.40	5.50	-	-
CR3/135	6.40	5.10	-	-
CR3/136	5.70	5.50	-	-
3410-10	5.10	5.50	-	-
3413-09	6.30	6.30	-	-
Batten	5.50	5.00	4.90	4.37
C7205 (CRAW 17	5.00	5.00	5.20	5.00
PBI 1908-49-5	5.90	5.00	4.90	4.40
P648,05(CRAW 50)	5.60	5.10	4.70	4.60
PBI 1908-49-7	5.80	5.00	4.70	4.60
P693,02	5.90	5.70	5.20	5.10
PBI 1013-13-3	5.30	5.00	4.80	4.16
3431-01	5.60	5.30	5.40	5.00
3458-34	5.60	5.80	5.30	4.70
3494-01	6.70	5.80	5.60	5.00
88PBI9	6.00	5.40	5.00	4.40
CRAW 45	5.80	5.20	5.90	5.00
PBI 1641-25	5.40	5.40	5.00	4.60
3415-20	6.60	6.60	5.50	5.10
Konini	5.80	5.50	5.40	5.02
3496-03	5.60	5.20	5.00	4.60
3665-30	5.60	5.50	5.30	4.90
3665-08	5.40	5.62	5.50	4.70
Otane	5.80	6.00	4.90	4.90
CR5/188(PSW 251)	6.10	5.70	5.50	4.90
CRSW 6(PSW 251)	5.80	5.80	5.60	4.90
CRSW 18	6.00	5.50	5.00	4.40
CRSW 19	6.00	5.90	5.10	5.00
CRSW 22	6.40	5.90	5.00	4.90
Genero 81	5.75	5.80	5.10	5.00
18-IBSWN-136	5.80	5.42	4.60	4.66
P694,03	6.00	5.80	5.00	4.30
Oroua	6.10	5.50	4.90	4.50
Karamu	6.06	5.10	4.70	4.40
Rongotea	5.90	5.37	5.50	4.70
Otane Rogue	5.50	5.50	5.70	4.90
Transvaal	5.77	5.80	5.40	5.50
S.F.A 1116	6.10	5.70	5.32	5.10
659/16	6.45	5.57	5.10	4.67
449,02/22	5.70	5.20	5.20	4.90
441,021	6.42	5.40	5.70	4.80
722,02	5.90	5.80	5.50	5.00

4.5 Response Pattern Analysis

4.5.1 Principal Component Analysis

The differences between spring and winter wheats are reflected in interactions of these various attributes across the four maturation environments. As the patterns are complex, and need to be considered as a whole, principal component analysis hase been used to ordinate the genotypes.

For each character in turn, the environment means were set up as attributes for each genotype (as entities). Principal components were then fitted to this data matrix, character by character, providing scores characterize the genotype X environment responses. They were fitted across environments (as variates) for each character thereby, giving a score characterizing the genotype X environment response for that attribute. The proportion of variation accounted by each component and their cumulative percentage, are presented in Table (4.29).

The first component indicates usually the general effects and the others may show contrast between variables (Morrison 1967). These data provided a basis for deciding on the number of component to be studied, using a benchmark of 70% of total variation explained (Morison 1967). The first two components satisfied this criterion (Table 4.29). In most of the characters more than 70% of the variation of the data were explained on the basis of first component.

The factor structure of the principal components enable the components to be interpreted and are given in Table 4.30 for all characters. The same basis structure was obtained for most of characters. There was a high to moderate positive correlation between first component and all environments. This indicated that the first component described the general effect of all environments, including any effect of temperature and daylength.

Table 4.29 Variance explained by the Principal Component Analysis.

	Component 1		Component 2		Component 3		Component 4	
Character	Prop.	Cumul.	Prop.	Cumul.	Prop.	Cumul.	Pro.	Cumul.
DFL	0.799	0.799	0.187	0.985	0.011	0.996	0.004	1.000
SPKN	0.738	0.738	0.170	0.908	0.066	0.974	0.026	1.000
FRAT	0.588	0.588	0.236	0.823	0.123	0.946	0.055	1.000
PL	0.858	0.858	0.068	0.926	0.045	0.971	0.029	1.000
LFN	0.665	0.665	0.318	0.984	0.016	1.000		
LAR	0.422	0.422	0.350	0.773	0.227	1.000		
TPR	0.391	0.391	0.339	0.725	0.275	1.000		

As explained earlier Characters LFN, LAR and were available only in three environments.

Prop. = proportion Cumul. = cumulative

Table 4.30 Factor Structure of the principal components.

Character	Comp.	ENV1	ENV2	ENV3	ENV4
DFL	1	0.924	0.957	0.980	0.681
	2	-0.365	-0.268	0.100	0.728
SPKN	1	0.279	0.320	0.314	0.244
	2	-0.678	-0.254	0.112	0.965
FRAT	1	0.815	0.905	0.811	0.457
	2	-0.387	-0.222	0.158	0.847
PL	1	0.926	0.924	0.955	0.898
	2	-0.235	-0.190	0.011	0.426
LFN	1	0.454	0.494	0.225	
	2	-0.418	-0.042	0.933	
LAR	1	0.806	0.783	0.065	
	2	-0.229	0.315	0.949	
TPR	1	0.709	0.766	0.287	
	2	-0.379	-0.004	0.926	

The correlation between component 2 and winter environments was negative for most of the characters, while it was positive for spring environments. This suggests a winter-spring contrast as the mining of the second component. Although this was often a minor component relative to the first (Table 4.30), the contrast was helpful in interpreting and positioning the response patterns of genotypes.

For character TPR, the correlation between component 1 and early winter environment as well as late spring environments was negative but it was positive for late winter environments. This means that tiller production rate is generally lower in cold temperature and short days as well as in high temperature and long days.

The genotype component scores are given in Table 4.31 and the scatter plots of the genotypes for first two components are shown in Figures 4.1 - 4.7 for characters LAR, TPR, DFL, LFN, SPKN, FRAT and PL respectively.

Genotypes with a large principal component scores were positioned in the extreme low or extreme high level of performance depends on the correlation level between its relevant component and variable (here environment). Those genotypes which their principal component scores are around zero were positioned in the middle level of performance.

4.5.2 Cluster Analysis

Using the cumulative proportion criteria discussed earlier, there were two scores describing each genotype's rsponse pattern and consequently genotype's habit. In order to identifying the "habit " of the genotypes and classifying them, the principal scores were subjected to a cluster analysis by Ward method.

Table 4.31 Principal components (C1, C2) scores of genotypes for each character

	LAR		TPR		LFN		DFL		SPKN		FRAT		PL	
Genoypes	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2
Batten	0.31	-0.70	-0.09	0.75	0.35	-1.17	-0.05	-1.04	-0.90	-1.61	0.08	-0.75	-0.36	1.20
C7205	0.72	-1.35	-0.65	-0.46	1.66	0.85	1.45	2.03	0.66	0.89	-1.43	-0.75	-1.75	-1.22
PBI 1908-49-6	-0.44	0.52	-0.39	0.56	1.59	-0.35	1.17	-1.01	2.00	-0.95	-0.76	1.19	-0.33	0.40
P648,05	-0.51	0.41	-0.75	0.59	1.47	-0.33	1.20	-0.99	1.82	-0.55	-0.61	0.55	-0.19	0.12
PBI 1908-49-7	-1.27	0.21	-0.76	1.08	0.17	-0.51	0.65	-0.76	1.31	-0.52	-0.93	0.39	-0.10	0.95
P693,02	-1.13	-0.13	-1.19	-0.11	-0.24	-0.70	0.63	-0.37	-0.12	-0.15	-0.71	0.52	-0.96	0.64
PBI 1013-13-3	-1.53	-0.61	-0.48	0.36	-0.20	-0.61	0.76	-0.33	1.73	-0.10	-0.20	0.67	-0.94	0.38
3431-01	-1.27	0.42	-0.20	0.13	0.80	-0.22	0.90	-0.90	0.66	0.01	-1.44	0.30	-0.28	0.70
3458-34	-0.09	-0.73	0.26	0.99	-0.07	-1.03	0.10	-0.54	-0.07	-0.50	-0.08	0.70	0.22	0.29
3494-01	0.06	0.81	-0.61	0.87	0.96	0.59	0.62	0.16	1.44	1.37	0.54	-0.15	0.63	0.79
88PBI9	-0.22	0.65	0.68	0.74	1.10	0.25	0.95	-0.36	0.49	0.47	-1.14	0.39	-0.25	0.75
CRAW 45	-0.05	-1.02	-0.58	0.99	_	_	2.68	2.73	1.21	0.67	-3.28	-1.42	-2.56	-3.31
PBI 1641-25	-0.14	0.59	-1.00	-0.15	1.11	-0.37	1.12	-0.83	2.15	0.06	-1.58	0.26	-0.69	-0.02
3415-20	-0.40	0.33	0.56	-0.04	0.56	-0.23	0.67	-0.97	0.43	0.09	-0.22	-0.38	-0.73	0.98
Konini	0.80	1.46	-0.15	-0.04	0.48	1.08	0.40	0.51	1.65	0.26	-0.05	0.71	0.35	-1.17
3496-03	-0.48	-0.48	-0.56	0.19	-0.23	-0.87	0.63	-0.09	-0.46	0.72	-0.54	0.57	-0.32	1.37
3665-30	1.41	0.21	-0.46	-2.49	1.61	0.90	1.00	0.92	-0.91	-0.38	-1.22	0.37	0.21	-0.04
3665-08	1.13	1.46	-0.45	0.86	1.15	1.05	0.30	0.42	0.39	0.02	0.09	0.75	0.26	-0.23
Otane	-1.49	0.02	-0.74	-0.19	-2.13	0.15	-1.41	0.18	-1.08	0.77	0.89	0.99	0.13	-0.65

Table 4.31 continued...

	LAR		TPR		LFN		DFL		SPKN		FRAT		PL	
Genoypes	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2
CR5/188	0.00	1.13	1.06	0.66	-0.71	0.72	-1.38	0.59	-0.59	0.61	1.01	-0.80	0.10	-0.49
CRSW 6	0.53	-0.18	1.01	0.90	0.65	-0.58	-0.02	-0.47	0.26	-0.96	-0.29	0.64	0.29	0.48
CRSW 18	0.52	-0.46	-1.19	1.47	0.05	-1.05	-0.47	-0.76	-0.64	-1.67	0.46	-0.20	0.15	0.77
CRSW 19	-1.09	-0.85	1.22	-1.43	-1.83	-0.08	-1.38	0.08	-0.22	0.71	0.97	-0.42	0.43	-0.96
CRSW 22	-0.28	-1.27	0.50	1.83	-0.41	-0.95	-0.23	-0.74	-0.71	-1.16	0.71	0.26	0.65	1.04
Genero 81	-0.22	2.07	0.80	-2.71	-0.57	2.71	-1.11	2.00	-0.61	1.93	1.03	-0.86	-0.90	-1.09
18-IBSWN-136	-0.82	0.04	2.83	-1.40	-1.36	1.07	-1.21	1.68	-0.68	1.91	-0.12	-1.95	-1.18	-0.01
P694,03	0.73	-1.74	1.03	-0.31	-0.37	-1.60	-0.72	-0.92	-0.12	-0.71	0.71	0.93	0.11	0.41
Oroua	0.15	-1.12	1.46	0.95	-0.47	-1.23	-0.74	-1.07	-1.52	-1.99	0.61	0.91	-0.26	1.00
Karamu	0.99	0.16	0.87	-1.02	-0.28	0.46	-1.19	0.14	-0.90	-0.28	0.35	-3.76	0.39	0.21
Rongotea	-0.50	-0.75	0.70	0.72	-0.26	-0.67	-0.16	-0.68	-0.80	-1.05	0.57	0.22	0.15	0.64
Otane Rogue	-1.04	2.86	0.34	-0.25	-0.60	2.67	-1.04	1.91	-1.40	1.79	0.83	0.97	0.95	-1.20
Transvaal	-0.48	1.37	2.30	0.07	-0.56	0.70	-1.19	0.17	-0.06	1.03	0.89	-0.41	2.77	-0.81
S.F.A 1116	-0.82	0.39	0.69	0.57	-1.41	0.76	-1.28	0.19	-0.42	1.00	1.62	-0.60	3.05	-1.90
659/16	0.04	-1.81	0.30	0.31	-1.00	-1.29	-0.85	-0.82	0.25	-1.17	0.93	-1.20	1.09	0.12
449,02/22	-1.86	-0.49	0.72	0.86	-1.69	-0.21	-0.81	0.54	-0.3	0.11	0.72	-0.55	-0.14	-1.32
441,021	-0.24	0.07	-0.23	1.09	-0.07	-0.14	-0.30	-0.69	-0.31	-1.10	0.93	1.00	-0.13	0.56
722,02	1.32	-0.04	-0.21	-0.14	0.76	0.21	0.31	0.07	-0.34	0.45	0.70	0.93	0.15	0.61
Se=(Eigh.)$^{1/2}$	1.12	1.03	1.08	1.00	1.41	0.98	1.79	0.86	1.72	0.82	1.53	0.97	1.85	0.52

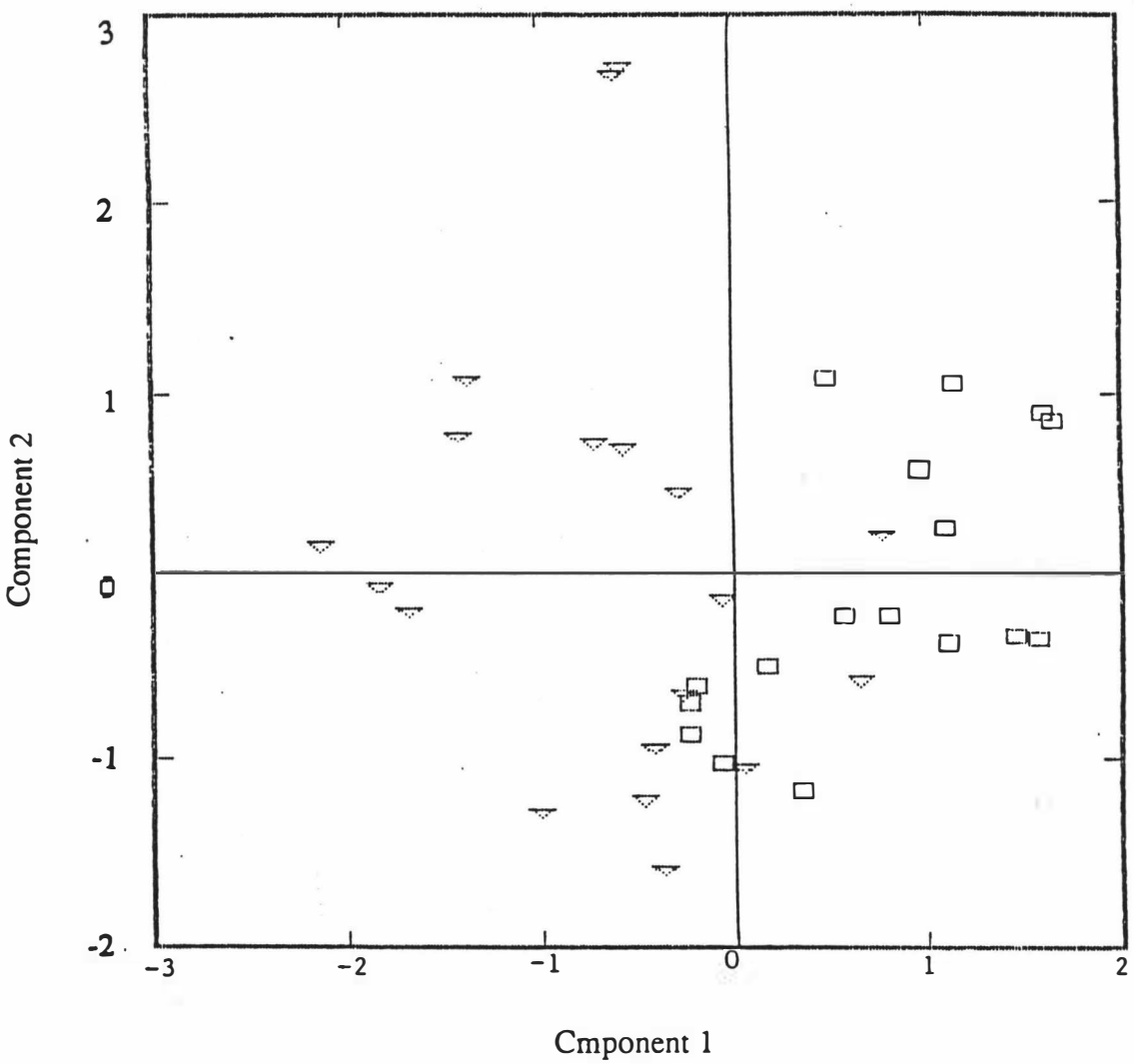


Figure 4.1: Distribution of the genotypes according to their response patterns on the basis of the first two principal component describing G X E means for Final leaf number.

□ Putative winter type

▽ Putative spring type

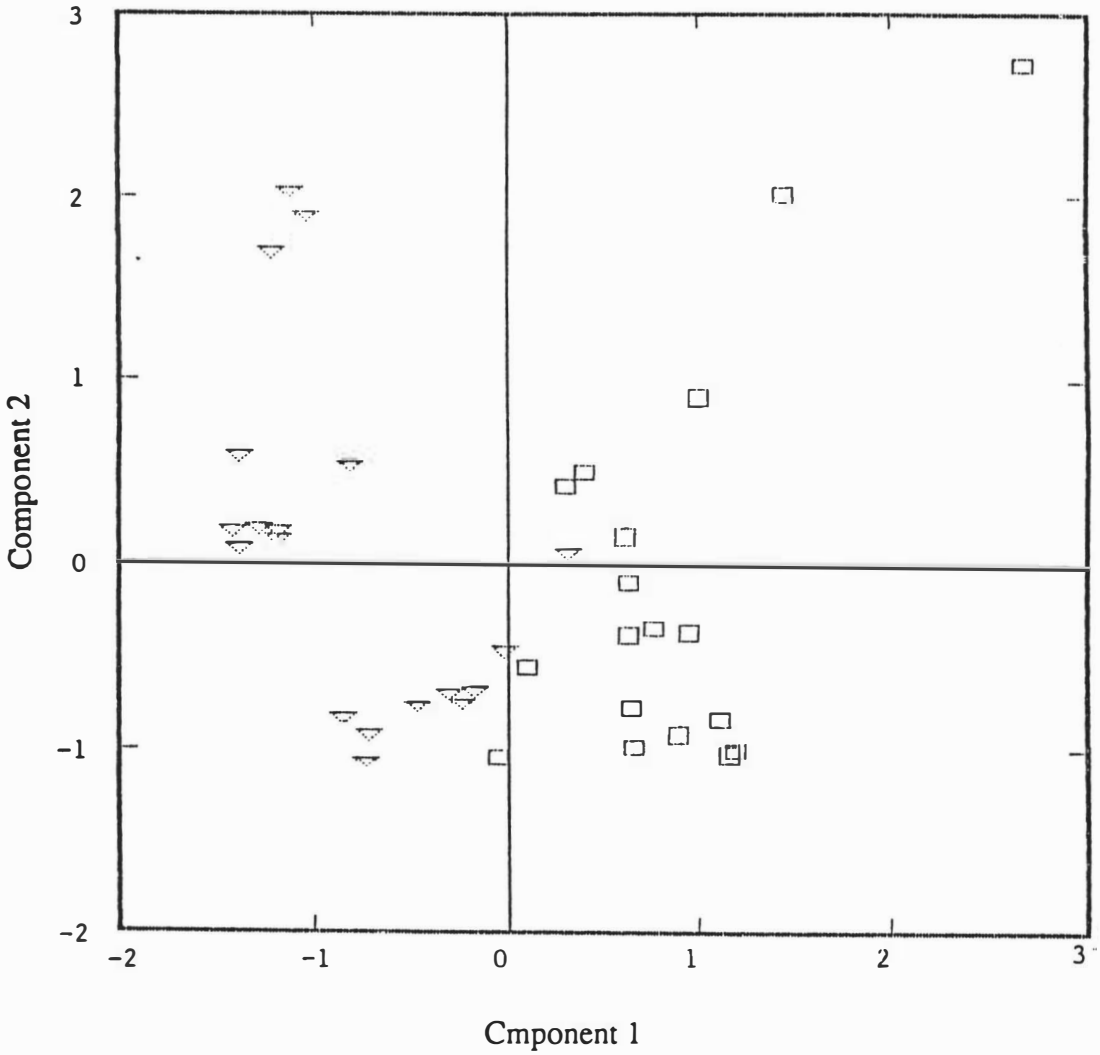


Figure 4.2: Distribution of the genotypes according to their response patterns on the basis of the first two principal component describing G X E means for days to flag leaf unfolding.

□ Putative winter type

▽ Putative spring type

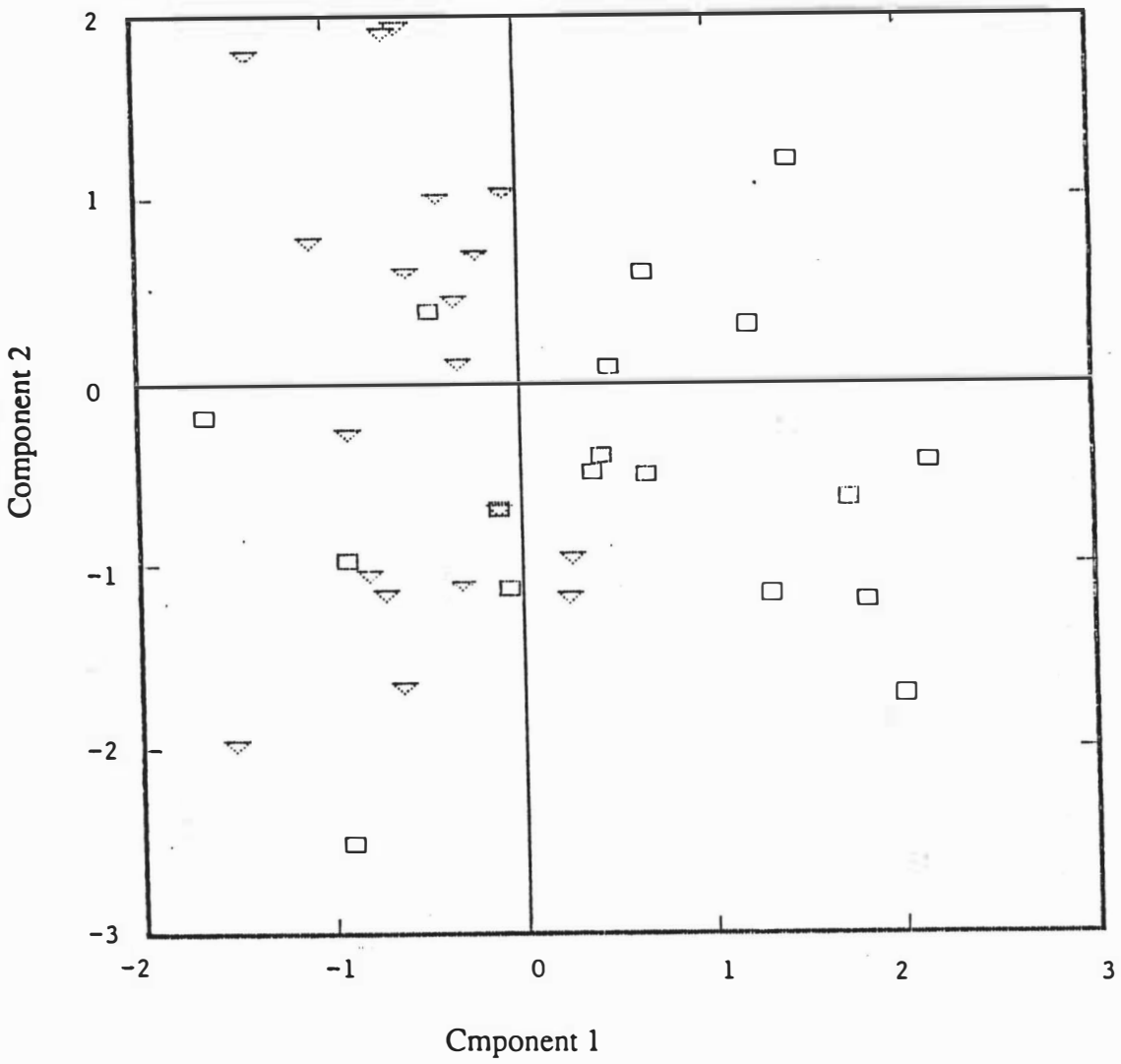


Figure 4.3: Distribution of the genotypes according to their response patterns on the basis of the first two principal component describing G X E means for the number of spikelet.

□ Putative winter type

▽ Putative spring type

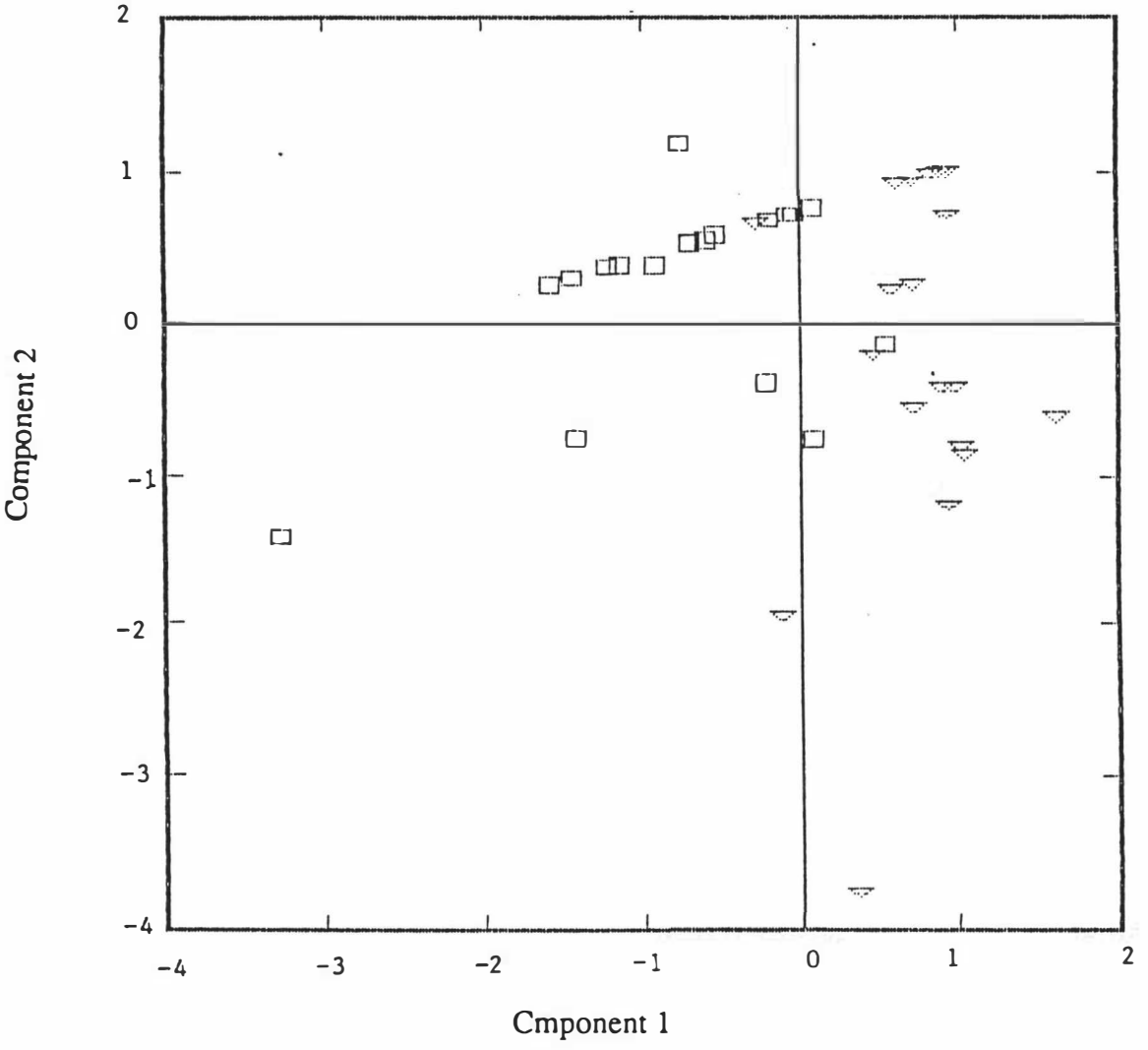


Figure 4.4: Distribution of the genotypes according to their response patterns on the basis of the first two principal component describing G X E means for fertility ratio of tillers.

□ Putative winter type

▽ Putative spring type

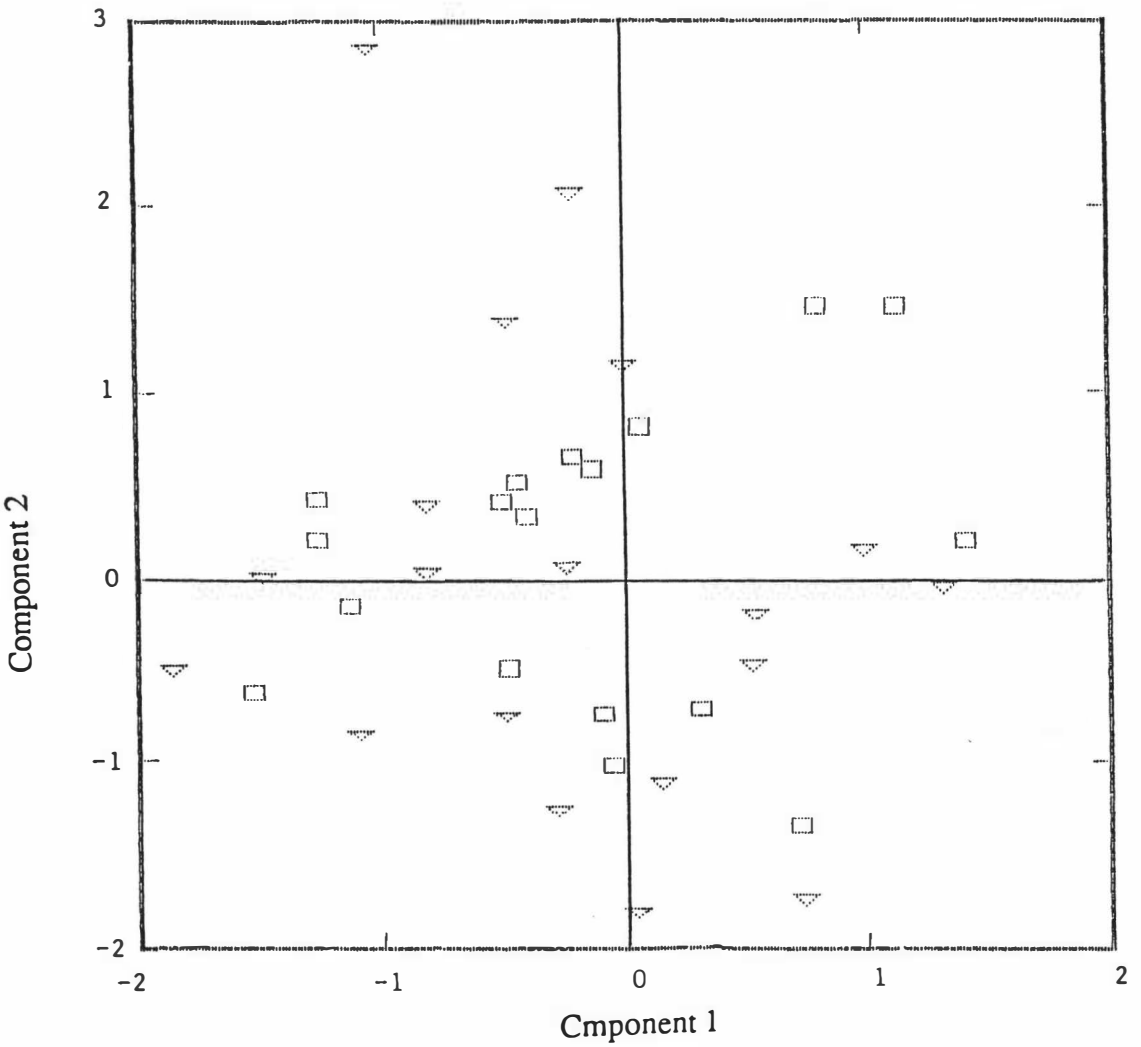


Figure 4.5: Distribution of the genotypes according to their response patterns on the basis of the first two principal component describing G X E means for leaf appearance rate.

□ Putative winter type

▽ Putative spring type

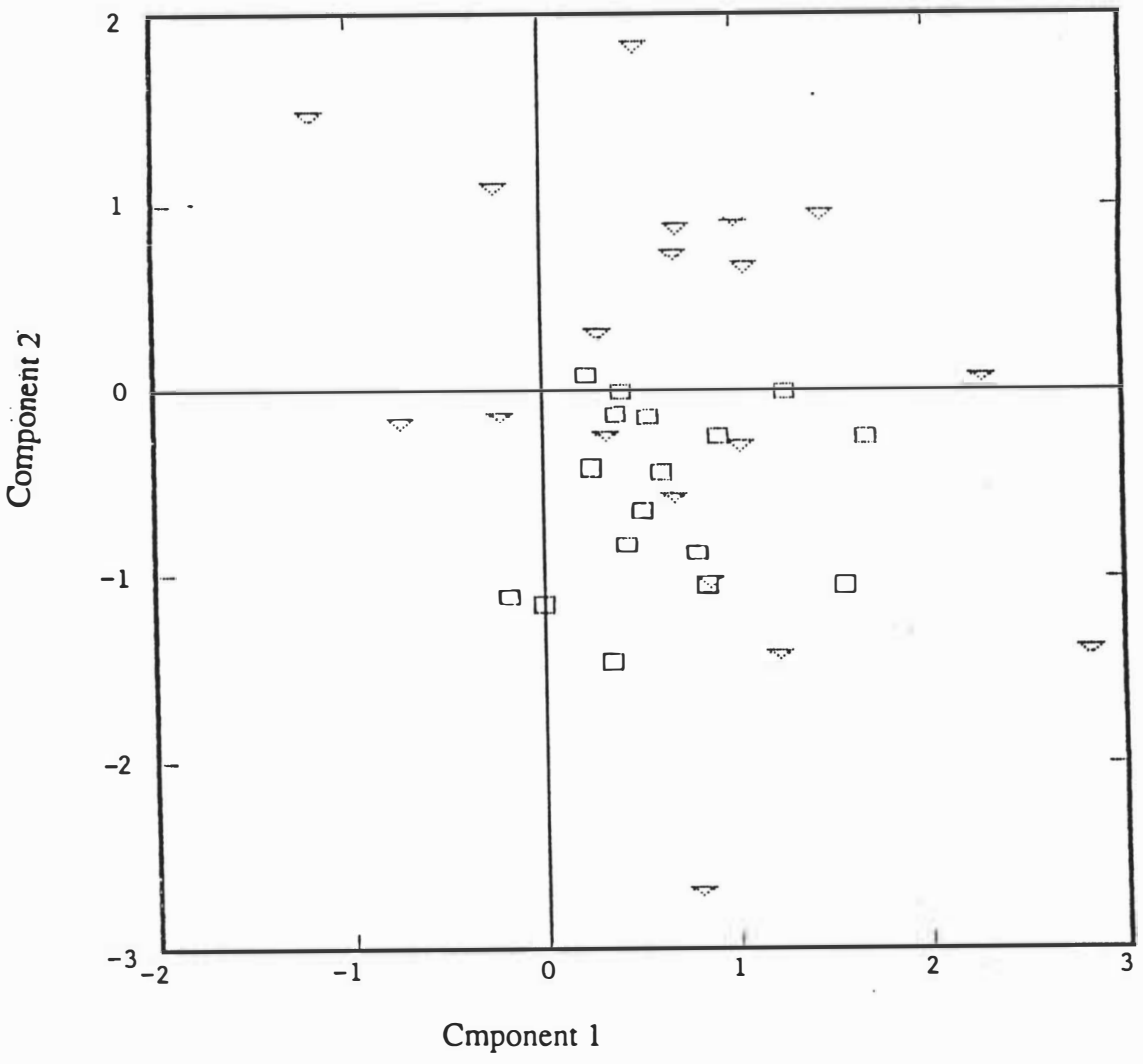


Figure 4.6:Distribution of the genotypes according to their response patterns on the basis of the first two principal component describing G X E means for tiller production rate.

□ Putative winter type

▽ Putative spring type

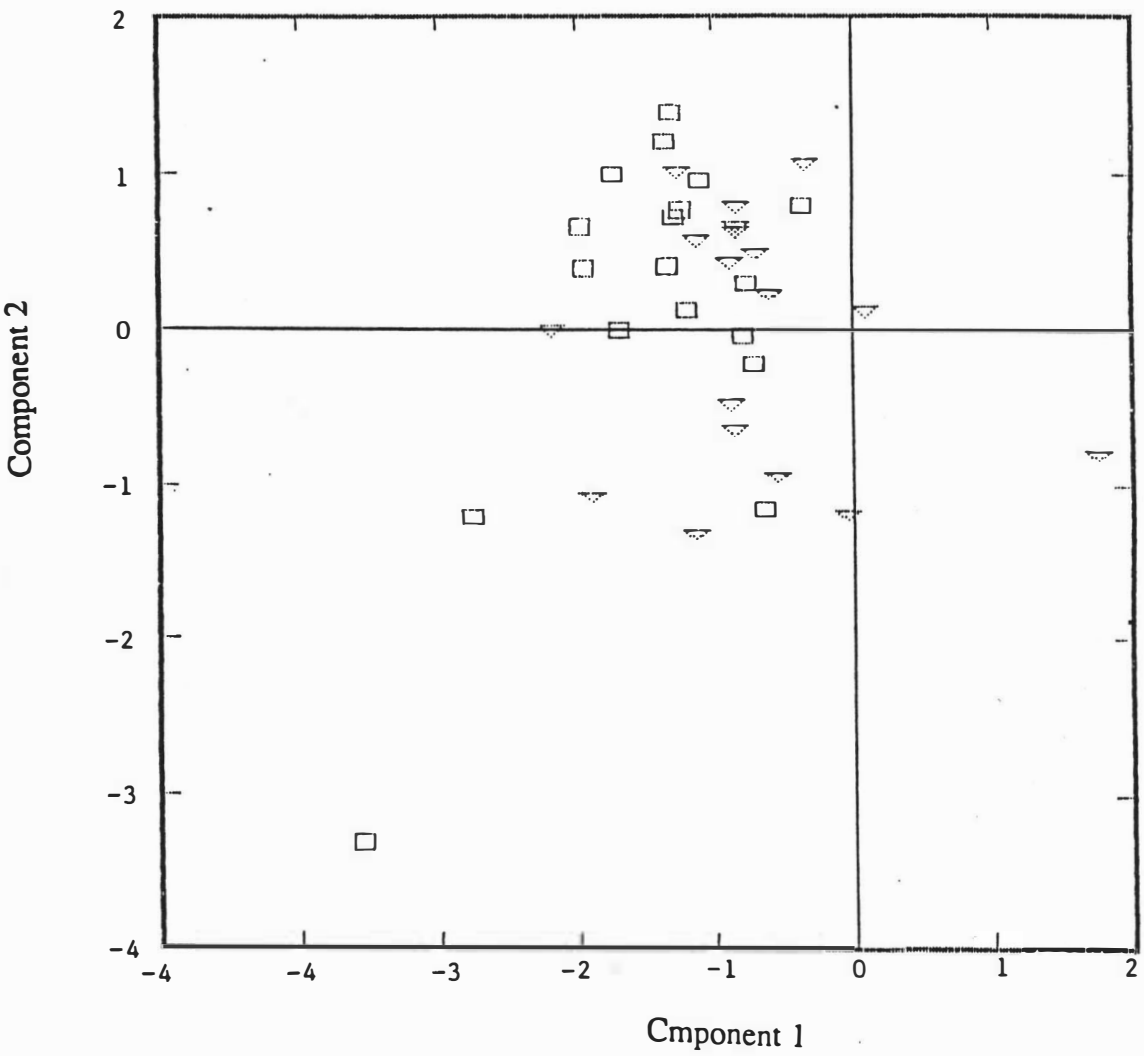


Figure 4.7: Distribution of the genotypes according to their response patterns on the basis of the first two principal component describing G X E means for peduncle length.

□ Putative winter type

▽ Putative spring type

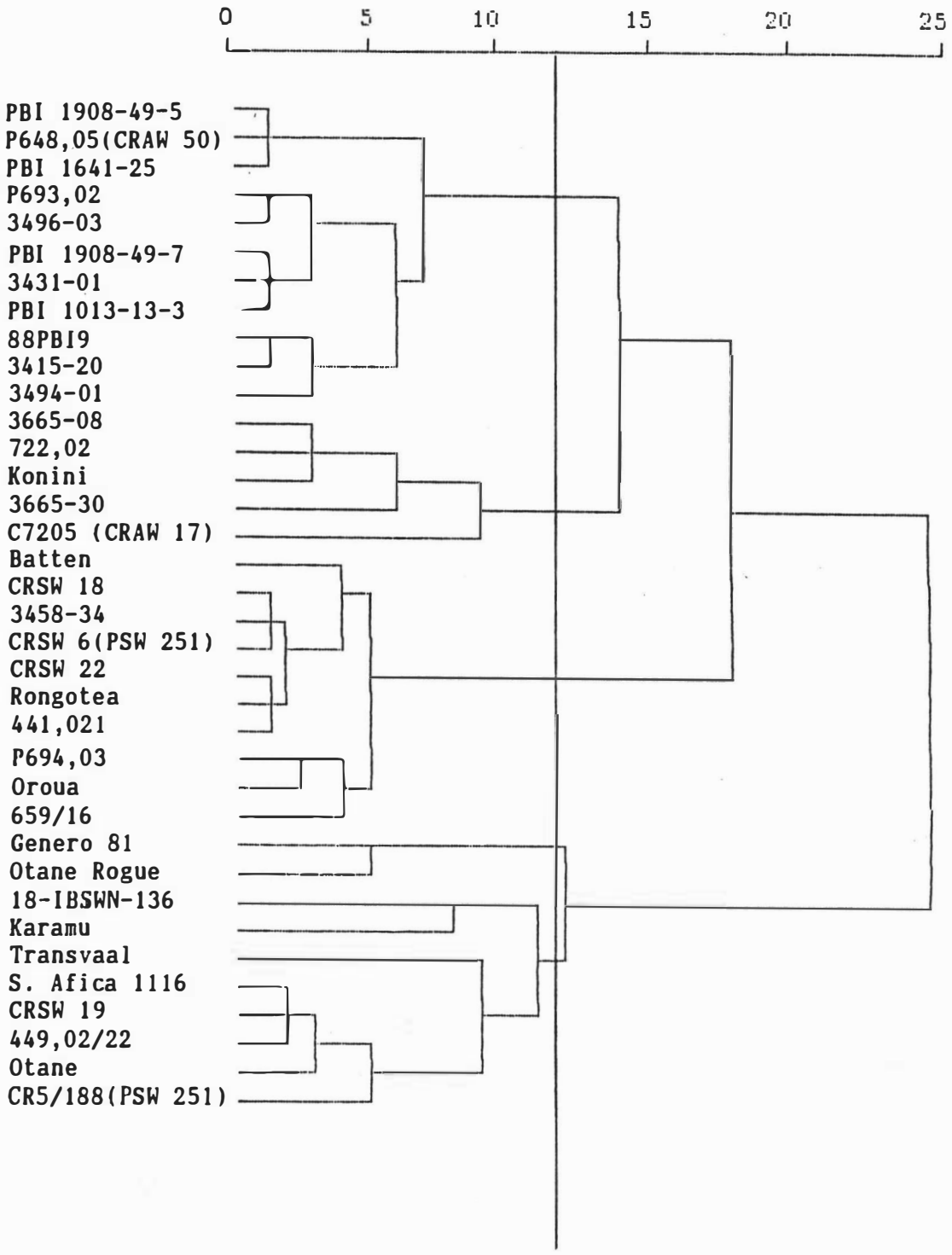
The method suggested by Gordon (pers. comb.), and used by Teow (1978) and Cullen (1981) was applied To determine the optimum location to truncate the dendogram, thereby defining the number of clusters. The probability of F test of the analysis of 5 cluster was minimum (Table 4.32).

As described earlier (chapter 3), optimum clustering is where the amongst-cluster mean squares is most significant relative to the within-cluster mean squares. This was examined through a post cluster analysis using the cluster identities (see chapter 3). It was done here on all attributes simultaneously (MANOVA), using Rao's F approximation of Wilks Lambda (Morrison 1967) for amongst-cluster significance. This was compared for several sequential clustering stages, the most significant defining the stage to truncate the dendogram (Table 4.32 and Figure 4.8).

Table 4.32 The probability of F test of each cluster.

Number of clusters	MANOVA DF	Rao's F Ratio	Prob.
2	(14, 21)	24.48	0.000,000,745
3	(28, 40)	15.47	0.000,000,035
4	(42, 57)	13.92	0.000,000,00366
5	(56, 72)	10.67	0.000,000,00210
6	(70, 85)	8.20	0.000,000,00242

Figure 4.8 Dendogam obtained by cluster analysis, using Ward method.



4.5.2.1 Interpretation of clusters

The mean principal components (PC1 and PC2) of each cluster for all 7 characters which are to be interpreted to describe the clusters are presented in Table 4.33. The interpretation was performed with regards to the position of a cluster on the basis of its mean for general performance in all environments (mean of pc1), and Interactive performance in spring and winter environments (mean of pc2). This interpretation will be used in discussion to determine the characteristics of clusters with respect to vernalization and photoperiod sensitivity and consequently habit.

Cluster means of studied characters which represents the responses of clusters to environments and will be used in discussion of habite differences and their effects on adaptive characters, are presented in Table 4.34. The average vernalization response of these clusters are also given in Table 4.35, as auxiliary information in comparison of the clusters vernalization responses estimsted by biometrical approach with that obtained by simple vernalization test.

Table 4.33 The means of principal component scores for each character in each cluster and their interpretation.

Cluster	LAR		TPR		PL	
	PC1	PC2	PC1	PC2	PC1	PC2
1	-0.666 MLG	0.247 SE > WE	-0.427 MLG	0.384 SE > WE	-0.378 MLG	0.642 SE >> WE
2	1.076 HG	0.348 SE > WE	-0.384 MLG	-0.454 SE < WE	-0.156 MG	-0410 SE < WE
3	0.117 MG	-0.864 SE < WE	0.375 MHG	0.870 SE >> W	0.191 MHG	0.651 SE >> WE
4	-0.630 MLG	2.465 SE >> WE	0.570 MHG	-1.480 SE << W	0.250 MG	-1.145 SE << WE
5	-0.696 MLG	0.221 SE > WE	1.119 HG	-0.378 SE < WE	0.694 MHG	-0.742 SE << WE

HG = High in general
HL = Low in general
M = Mediume

SE = Spring Environment
WE = Winter Environment

< > Lower or higher
<< >> much lower or higher
'=' Slightly the same

Table 4.33 continued.

	LFN		DFL		SPKN		FRAT	
Cluster	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
1	0.645 HG	-0.304 SE < WE	0.845 HG	-0.586 SE < WE	1.043 HG	0.041 SE'='WE	-0.690 LG	0.392 SE > WE
2	1.132 HG	-0.818 SE << WE	0.692 MHG	0.790 SE >> WE	-0.370 MG	0.248 SE > WE	-0.382 MLG	0.402 SE > WE
3	-0.160 MG	-0.971 SE << WE	-344 MLG	-0.773 SE < WE	-0.456 MG	-1.192 SE << WE	0.463 MHG	0.251 SE > WE
4	-0.585 MLG	2.690 SE >> WE	-1.075 LG	1.970 SE >> WE	-1.005 LG	1.860 SE >> WE	0.930 HG	0.055 SE '='WE
5	-1.246 LG	0.446 SE > WE	-1.231 LG	0.446 SE > WE	-0.532 MLG	0.733 SE >> WE	0.791 HG	-0.937 SE << WE

Table 4.34 Group means in environments for all studied Characters

Cluster	Env 1	Env 2	Env 3	Env 4
Days to flag leaf unfolding:				
WW	132.53	120.56	NF	NF
1	129.66	111.08	67.59	47.54
2	123.17	106.82	67.20	52.56
3	118.90	102.31	60.05	42.55
4	100.59	90.95	57.25	50.75
5	104.97	92.16	56.31	43.80
Days to heading:				
WW	150.08	137.40	NF	NF
1	146.12	126.46	82.09	63.26
2	140.90	121.94	80.90	65.04
3	136.49	117.40	73.70	53.75
4	117.66	106.95	71.00	60.44
5	120.57	108.52	69.12	54.96
Days to anthesis:				
WW	152.90	139.34	NF	NF
1	150.11	130.01	85.04	67.36
2	145.37	125.78	83.70	69.12
3	141.20	121.67	76.95	58.88
4	122.91	112.12	74.50	66.21
5	127.32	113.34	72.87	59.83

ENV = Environment, WW = True winter wheats (N.F in spring sowing)

Table 4.34 continued:

Class	Env 1	Env 2	Env 3	Env 4
Peduncle length:				
WW	286	263	NF	NF
1	331	316	323	293
2	361	336	322	284
3	348	340	369	313
4	375	345	346	272
5	404	366	385	310
Main stem height:				
WW	690	608	NF	NF
1	778	696	689	582
2	821	746	752	638
3	871	768	802	599
4	794	803	816	599
5	891	810	808	640
Internodes number:				
WW	5.91	5.44	NF	NF
1	5.85	5.40	5.07	4.68
2	5.54	5.48	5.38	4.92
3	6.01	5.56	5.20	4.62
4	5.62	5.65	5.40	4.95
5	5.91	5.60	5.09	4.92

Table 4.34 continued:

Class	Env 1	Env 2	Env 3	Env 4
The number of spikelet:				
WW	24.3	24.05	NF	NF
1	24.67	23.70	22.41	19.82
2	22.23	20.56	20.24	18.47
3	23.69	20.72	19.83	16.97
4	19.02	19.02	19.81	19.16
5	21.58	20.00	20.00	18.84
Fertility ratio of tillers:				
WW	0.654	0.441	0.041	0.025
1	0.451	0.476	0.511	0.493
2	0.548	0.453	0.453	0.453
3	0.643	0.643	0.643	0.483
4	0.757	0.757	0.611	0.611
5	0.763	0.755	0.660	0.564
The number of fertile tillers:				
WW	6.49	5.51	0.6	0.35
1	6.60	5.50	5.69	5.39
2	7.82	5.87	6.16	5.62
3	5.60	5.64	5.17	7.55
4	4.85	6.00	5.50	5.55
5	7.55	5.31	5.20	4.52
The number of total tillers:				
WW	10.10	12.4	NF	NF
1	11.17	8.93	9.67	9.54
2	11.22	9.12	10.56	10.05
3	9.40	7.85	7.99	8.67
4	5.36	7.15	8.50	8.60
5	8.16	6.40	7.77	8.01

Table 4.34 continued:

Class	Env 1	Env 2	Env 4
Leaf number:			
WW	12.72	13.15	con.
1	11.91	10.61	8.67
2	11.95	10.93	9.70
3	11.33	9.97	7.88
4	8.92	9.57	10.41
5	9.33	9.08	8.51
Leaf appearance rate:			
WW	0.1063	0.1337	0.1432
1	0.1020	0.1140	0.1607
2	0.1147	0.1255	0.1613
3	0.1098	0.1161	0.1437
4	0.0883	0.1302	0.1834
5	0.0954	0.1202	0.1538
Tiller production rate:			
WW	0.0082	0.0195	0.0330
1	0.0205	0.0164	0.0431
2	0.0190	0.0168	0.0314
3	0.0103	0.0161	0.0493
4	0.0120	0.0187	0.0373
5	0.0111	0.0195	0.0451

Table 4.35

The mean differences of time to flag leaf emergence in unvernalized and vernalied plants and vernalization responses for each cluster and the type of wheatsin each cluster according to this factor.

Clusters	difference days=unver-ver	Generall response to vernalization
A	No fl.	Strong vernalization requirement
1	0.15	No vernalization requirement
2	6.5	Vernalization requirement
3	-0.30	No vernalization requirement
4	8.75	Vernalization requirement
5	1.87	Very weak or no vernalization requirement

Chapter 5

DISCUSSION

The following discussion interprets the main findings of the investigations of the responses of different genotypes to daylength and temperature in natural conditions. Genotypic variation in the influenced characters such as leaf number, time to flag leaf unfolding, etc.. and their interaction with environment will also be discussed. The implications of the results, both for wheat breeding programs and for further understanding of the genetic and physiology of wheat adaptability, will be discussed. Suggestions for further experiments will be presented.

5.1 Genetical Studies

5.1.1 Genetic Variation

In analysis (a), 37 genotype over all environments, a high level of significant genotypic effect of all characters (Table 4.6) proves the presence of considerable genetic variation for those attributes. Genotypic variance is the genetic variation between cultivars means. The total genotypic variance may be partitioned into additive, dominance and epistatic variance components (Griffing 1956; Cockerham 1963; Falconer 1981; Baker 1986). Since wheat is self-pollinated and the examined germplasm have been self pollinated for a long time, dominance variance approaches zero. Therefore, most of the genotypic variance estimated in this study was due to additive and additive * additive gene action.

On the other hand, macro environmental effects were also highly significant for all characters. This indicates that, the environments (sowing dates) were different, and all characters were highly affected by environmental factors (temperature and daylength). For attributes indicating the rate of development; days to flag leaf unfolding, ear emergence and anthesis, leaf appearance rate, and tiller production highly significant genotypic variability was observed: however, their environmental variances also were very large, and were much bigger than their genetical variance components (Table 4.6). Therefore it was confirmed that the rate of development was controlled mostly by environmental factors, temperature and daylength, compared to genetical factors (Kirby and Appleyard 1984, 1987; Hay and Kirby 1991).

Although the estimates of block (meso-environment) variance were low in comparison to genetic and macro-environment components, it was significant for all characters except the number of leaves. This may suggest that leaf number is relatively unaffected by block conditions such as soil heterogeneity. Therefore, it could be one of the reasons for preference of leaf number in investigation of vernalization and photoperiod responses in wheat to the other attributes by Hay and Kirby 1990. Variance component of block for TTN is markedly bigger than other components that may indicate that total tiller number is highly affected by meso-environment such as soil and plot conditions.

The variance component of genotype X environment interaction was non-significant only for characters FTN, TTN and MSH. The interaction reveals that all genotypes are not responding in the same way to the changes in sowing date. This is the key component in this study, as it indicates that different responses to changing seasonal condition (including temperature and photoperiod) are presents among these genotypes (Table 4.6). Most of the studied characters were also responsive to vernalization temperatures (low temperatures) and

daylength in natural condition (Table 4.6). The non-significant genotype X environment variance for characters FTN, TTN, MSH may indicate that these characters are controlled almost genetically, and are affected by temperature and photoperiod in a same direction in examined natural environments.

The proportion of genetic variance to environment variance in analysis of 43 genotypes over two environments (analysis b) was larger than in analysis (a) (Tables 4.6 and 4.7). On one hand, because, the environment variation was larger in analysis (a) including 4 winter and spring environments than in analysis (b) including only 2 winter environments. On the other hand, because, genotypic variation in analysis (a) excluding strong winter types was smaller than in analysis (b) including those strong winter types.

The considerable differences between estimates of variance components in these two sets of analysis have been caused by difference in sampling of environment and genotypes. The highly significant environment variance in analysis (b) as well as analysis (a), may suggest that the considerable variation in temperature and daylength can be achieved even by less spacing between the sowing dates. Therefore, close spacing between sowing dates and omitting the late sowing may provide quantitative performances for all characters even for true winter types.

5.1.2 Heritability

The heritability estimates obtained in this study were narrow sense as discussed earlier because, wheat is a highly inbred crop. Both a full and restricted heritability were estimated, as mentioned earlier. The full heritability estimates the genotypic variation as a fraction of overall phenotypic variance. The restricted type, which has been more commonly used in literature (Allard 1960) is the proportion of genotypic variance to only those parts of phenotypic

variance which genotype responses in a simple experiment (genotype X environment interaction, error and genotype variances). Because of the importance and magnitude of macro environment effects in growth habit responses the use of restricted heritability for these attributes seems to be an unrealistic approach.

In analysis (a), genotypic variance components for all characters were significant, but full heritability estimates were only moderate for traits TTN, FRAT, MSH and PL (31-57%), and were low for the rest of the attributes. This arose because, the environments were established deliberately to be effective on growth habit, and consequently their effects were large (e.g. σ_B and σ_E). This occurred particularly for the most pertinent traits, such as DFL, DHD and DANT. While Blum (1988) and Ehdai (1989) reported a high level of heritability for time to ear emergence regardless to vernalization and photoperiod responses.

Although, the full heritability of final leaf number was relatively low in analysis (a), but it was still six times bigger than the heritability of flowering characters. This was considerably high (72.4%) in analysis (b) and about twice bigger than flowering characters in this analysis. This suggests again that character, LFN is more appropriate than flowering attributes in selection for growth habit as Hay and Kirby (1991) have reported .

In analysis (b), becausethe range of variation of environments was restricted to only two winter environments and genotypic variation included the strong winter types, full heritability was much larger than in analysis (a). For example, full heritability of flowering characters was very low in analysis (a) but, it was moderate to high (35-72%) in analysis (b), (Tables 4.8 and 4.9).

This observation of the difference between the heritability estimates

obtained by these two sets of analyses is a feature of all research which depends on sampling. Hanson (1963) pointed out that any generalization of heritability to other populations should be done cautionsly. In this case, a divers germplasm has been used, and the environment range has been widly sampled, so, that the present results have a considerable degree of confidence.

Presence of low full heriability for the most physiologically related characters to type of wheat, indicates that they are influenced largely by environment. Therefore, in selection for vernalization and photoperiod sensitivity or insensitivity, using a group of these attributes as criteria may be more effective than using one character alone. The criteria in selection for growth habit should have two important characteristices: considerable response to vernalization and photoperiod, and higher heritability. Selection indices can be designed considering these two characteristics in further studies. According to genotype X environment variance and heritability estimates, characters FRAT, LFN, SPKN were more responsive and heritable than the others (Tables 4.6, 4.8, 4.9).

5.1.3 Phenotypic and Genotypic Correlation

Phenotypic and genotypic correlations are important to plant breeders in selection, indicating how correlated responses will occur. To physiologists they asist understanding correctly the interplay of characters, although partial-correlation would be useful for that purpose. The observed simple correlation which is measured directly (phenotypic) is a compound of genotypic and environmental components (Falconer 1981), and it will not be useful on its own in a selection program. Genotypic correlation arises from linkage, pleiotropy, or shared, and genetically defies physiological pathways between the two characters (Simonds 1979). It is an essential aspect of predicting correlated

selection responses amongst a group of attributes. Such correlations can be used also for judging the efficiency of indirect selection (selection as character other than one of prime interest) in achieving one's appeals.

In the present study, in both sets of analysis, a very high level of positive phenotypic and genotypic correlations were observed between the flowering traits, DFL, DHD and DANT (0.98-0.998) (Tables 4.10, 4.11, 4.12 and 4.19). It may suggest that the three stages of wheat development (flag leaf unfolding, ear emergence and anthesis) are controlled in fact by the same process and that characters DFL, DHD and DANT are different aspects of that same basic attributes. Therefore, any one of these stages is equally useful but, days to earlier stage (days to flag leaf) will be used for further discussions here. In most of the previous growth habit studies, the attribute days from sowing to ear emergence was applied to measure the vernalization and photoperiod responses (Hoogendorn 1984; Flood 1983). These results suggest that an earlier measure (flag leaf emergence) would be just as useful.

Days to flag leaf has been used for this purpose by several workers (Takahashi and Yasuda 1956; Gotoh 1967, 1983). Days to anthesis also has been used by Halse and Wair (1970). Levy and Peterson (1972) and Kirby (1990) used the number of leaves in their growth habit studies, because they cosidered that time to flag leaf, ear emergence and anthesis were functions of leaf number. Hay and Kirby suggested that the influence of vernalization can be interpreted more clearly from the results of leaf number analysis. In this study, there was a highly significant genotypic and phenotypic association (0.81-0.91) between leaf number and these timing traits (Tables 4.9 and 4.10).

Character SPKN had also significantly positive both genotypic and phenotypic correlation with flowering characters and leaf number (0.65-0.75). It may suggest that a plant with more leaves will produce more spikelets, and the

time of flowering will be delayed. This tends to confirm the report by Rahman and Wilson (1977) that an increase in spikelet number was associated with longer duration of both vegetative and spikelet phases.

Total tiller number is associated positively with leaf number and flowering characters, and negatively with the ratio of fertile tillers to total tillers (FRAT). This confirmed that the number of emerged tillers is partly associated with the number of leaves on main stem (Masle 1985: Hay and Kirby 1991). A high negative correlation genotypically between character FRAT, flowering attributes and leaf number (0.70-0.90) indicates that FRAT can also be an appropriate indicator for vernalization and photoperiod responses.

Tiller production Rate (TPR) has shown highly negative phenotypic correlation with flowering characters and moderate negative with leaf number. However, the genottypic correlation was very low and non-significant between them. The genotypic and phenotypic associations between leaf number and tiller number partly confirm the hypothesis that tiller production increases with increasing the number of emerged leaves, and therefore winter types may produce more tillers than spring types (Flood and Halloran 1986; Kirby and Appleyard 1987).

5.2 Genotypic Response to Environment and Growth Habit

The environments in this study were formed by changing sowing date (see chapter 2). Each environment includes a specific range of temperature and photoperiod (chapter 3). The responses of given genotypes to these environments are discussed in this section, followed by discussion of vernalization requirement and photoperiod sensitivity of genotypes in the next sections.

5.2.1 Timing of Development

As discussed earlier, timing of development in terms of days to flag leaf (DFL), ear emergence (DHD) and anthesis were highly correlated (genotypically and phenotypically) with the number of leaves on main stem, and phenotypically highly correlated with leaf appearance rate. The physiological dependence of timing of development on leaf number and leaf appearance rate has also been discussed by Levy and peterson (1979), Kirby and Appleyard (1987), Hoogendorn (1985) and Hay and Kirby (1991) previously. The functional relationship between leaf production characters and time to flag leaf can be defined as follows:

Time to flag leaf = The number of leaf + Leaf appearance rate

Timing of development was studied here using attributes: days to flag leaf, ear emergence and anthesis. It was discussed earlier that these three characters are probably different measures of one system and are also highly correlated with the number of leaves on main stem. Therefore, only DFL is considered further here. Days to flag leaf varied in each environment, and with genotype. It was reduced significantly with increasing temperature and daylength from the winter environment to the spring environment for most of the genotypes.

Genotypes Avalon, C3640, CR3/135, CR3/136, 34010-10 and 3413-09 did not complete their vegetative phases in the two spring environments, not even to the very end of the growing season. This suggested the presence of strong vernalization genes in those genotypes. It may also confirm that, generally, the higher the temperature the faster the rate of development, but winter types need to be vernalized in a period of cold to develop properly (Evans 1975; Kirby and Appleyard 1984, 1987).

While reduction of days to flag leaf for genotypes Genero-81 and 18-

IBSWN-136 was significant from first sowing to second sowing, it was not significant from third to forth sowing. This could be because of their vernalization requirement. Very high significant reduction of DFL from winter environment with short days to late spring environment with long days is expected for photoperiod sensitive genotypes. It was observed in genotypes such as CROW 49, CROW 50, P69302, and others (Table 4.16).

Lateness or earliness of a genotype in an environment is mostly due to the presence of vernalization and/or photoperiod genes (Klaimi and Qualset 1973,1974; Gotoh 1983 Hoogendorn 1984). The difference between days to flag leaf in unvernalized and vernalized plants, grown under natural long days, was used to recognise the presence and the strength of vernalization response in this wide germplasm (see chapter 3).

Different levels of vernalization response were observed using the difference between days to flag leaf in vernalized and unvernalized seeds in sowing date 4. Six genotypes were not induced to floral reproductive phase in unvernalized plants. Many of the assumed spring wheats have shown some apparent vernalization response; and some of the assumed winter genotypes were not apparently responsive to vernalization. However, some may had photoperiod sensitivity and be late to mature (Table 4.4).

5.2.2 Leaf Production

5.2.2.1 The number of leaves

It was reviewed that genotypes with vernalization response are unable to flower until their vernalization has been satisfied, and continue to produce more leaves. Therefore, number of leaves produced in spring sowing would be more than in winter sowing, because the temperature is not low enough to complete

vernalization requirement. Genotypes with photoperiod sensitivity produce more leaves in winter (short days) sowing than in spring (long days) sowing (Halse and Weir 1970; Levy and Peterson 1972; Ford *et al* 1981. Hay and Kirby (1991) also suggested that leaf number gives more accurate indication of vernalization and photoperiod responses.

Six of the seven genotypes, which produced the highest number of leaves in winter sowing, were not induced to flower in the spring sowing and on of them (CRAW 45) flowered very late on a few tillers. Three other genotypes (Genero 81, Otane rogue, 18-IBSWN-136) were response suggestive of vernalization, in that they produced more leaves in the late spring environment than in the earlier sowing. They may have moderate vernalization response.

Many of the genotypes, which produced significantly more leaves in winter sowing than in spring sowing, were indicated as photoperiod sensitive (Table 4.19). In genotypes Otane, Transval, South Africa-1116, PSW 251 and Karamu, leaf number in spring sowing were slightly less than winter: they may have a very weak or nil vernalization requirement, and no photoperiod sensitivity.

5.2.2.2 Leaf appearance rate

Leaf appearance is controlled mostly by temperature (Hay and Tuniclife Wilson 1982). This was confirmed in this study, as the rate of leaf appearance was increased with increasing temperature from winter sowing to late spring (Table 4.20). However, Baker *et al* (1980) reported that leaf appearance may also be affected by changing daylength.

While genotypic and genotype X environment interaction variances were highly significant for this trait, its heritability tended to be low and the differences in response pattern of genotypes across the environments were not

interpretable clearly. Therefore, principal component and cluster analysis were used to solve this problem which will be discussed later.

5.2.3 Tiller Production

The sequence of tillering in winter wheat is similar to spring wheats; but, because the growth period is extended, more leaves produced on main stem in winter wheats and they may produce more primary tillers (Kirby and Appleyard 1984, 1987; Hay and Kirby 1991). It was observed that putative winter types in this study produced relatively more tillers than putative spring types. The extension of the vegetative phase in the spring sowing of winter types (because of the lack of required vernalization), increased the number of leaves and also the number of tillers. Genotypes which produced fewer tillers in spring environment than in winter environments may be spring wheats, with or without photoperiod sensitivity (Table 4.24).

While the number of total tillers in putative strong winter types was more than in putative spring types, the rate of tiller production in the winter types was lower than in the spring types. Rate of tiller production was generally increased with increasing temperature in later sowings (Table 4.21).

Vegetative tillers are changed to fertile tillers when satisfaction of the vernalization requirement occurred in shoot apices in winter wheats (Kirby and Appleyard 1987). Therefore, fertility of tillers in winter wheats depends on the degree of satisfaction of the vernalization. In this study, six strong winter genotypes did not produce any fertile tillers in spring sowings. Also one other genotype (CRAW 45) produced only 2.5 fertile of 15.3 total tillers in average in late spring sowing.

Generally the number of fertile tillers is reduced by shortening the duration

of the growth cycle from winter to spring environments for all genotypes (Table 4.23). On the other hand the association between number of fertile tillers and environment is not interactive, as shown by non-significant G X E variance estimates. Therefore this character alone may not be a good criterion to study the response to vernalization in a number of genotypes.

5.2.4 Fertility Ratio of Tillers

The ratio of fertile tillers to total tillers was used to separate the response of vernalization and photoperiod from the general effect of temperature (general shortening of the duration of the growth cycle) in this study. Recognition of genotypes with moderate vernalization response and genotypes with photoperiod sensitivity is possible using this ratio. That is, genotypes with reduced ratio from first sowing to fourth sowing may have vernalization requirement, because the requirement has not been satisfied in many tillers and they would not be induced. Examples included CROW 45, CROW 17, CROW 18, CROW 19, Konini (Table 4.25).

Genotypes with about the same ratio from winter to spring environment may be spring types with weak or no vernalization response (e.g Otane, Karamu). Genotypes with increased ratio may be photoperiod sensitive without vernalization requirement. This is because photoperiod requirement could be satisfied in long days in spring, following induction of flowering, leading to an increase in the ratio. Such in genotypes included CRAW 50, P693/02, 343-01, 88PBI9, etc... (Table 4.25).

5.2.5 Main Stem Elongation

The influence of growth habit on the elongation of main stem was studied

by using three characters: height, peduncle length and the number of visible internodes. Main stem elongation did not occur in the six strong winter types; and it was reduced in all of the genotypes from winter to spring as expected. This probably arose because of the increased temperature and day length, with consequent shortening of the growth cycle. Assumed spring types were generally taller than assumed winter types.

The result reported by Worland *et al.* 1987 that pleiotropic effects of the **Vrn1** gene increases plant height in longer growing periods, may need to be reconsidered. The changes in height were not significant from first sowing to third sowing, but in forth sowing it was reduced significantly for all genotypes, because of the marked increase of temperature in early summer (Table 4.26).

Peduncle length was changed slightly in a similar way to main stem height (Table 4.27). However, genotype X environment interaction was highly significant for peduncle length but not for height. Reduction in height was due firstly to reducing the internode length, particularly the peduncle, and secondly to reduction the number of internodes. The hight of a main stem is largely dependent on the length of peduncle internode (Kirby and Appleyard 1984). Any clear pattern of response to vernalization or photoperiod was not discernible in these characters.

5.3 Multivariate Analysis of G X E Interaction and Classification of Germplasm

The previous discussion made several interpretations about vernalization and photoperiod on the basis of one attribute at a time, by examining trends across environments. Since temperature and photoperiod effects are confounded in field conditions, analysis of net phenotype effects across genotypes do not give clear indications of presence and strength of vernalization and photoperiod

sensitivity in the genotypes.

Considering character DFL as an example, extreme increase from winter to spring sowing indicates strong winter types, and extreme decrease indicates photoperiod sesitivity, but genotypes with moderate response cannot be distinguished from insensitive genotypes by using this character solely. Another example comes from LFN. Increas in leaf number generally shows vernalization response; but, for genotypes with vernalization response and photoperiod sesitivity leaf number may not be changed significantly or even may be decreased (e.g. genotypes Konini and CRAW 17, Tables (4.4 and 4.19), and give result similar to spring wheats.

Therefore, it was desired to combine formerly those attributes considred to be particularly pertinent to clarifying plant form, and which had shown significant genotype X environment interaction (Tables 4.6 and 4.7). The genotype X environment means were set up to ordinate the lines according to the across-environment pattern of response.

The genotypes were set up as entities and the four environment means were arranged as variables, and principal component analysis was done separately for each character LAR, TPR, LFN, DFL, SPKN, FRAT and PL. The resulting first two principal components from each character were then clustered to delineate the genotype groupings. These analyses were used subsequently to identify groups of similarly responding genotypes over the environments tested.

The advantages of these two multivariate techniques in interpreting genotype X environment interactions have been discussed elsewhere (Eiseman *et al* 1977).

Most of the variation in each character was explained by the first two of

four principal components (Table 4.29). The first component usually represented a general score of the across-environment trends; that is, it was strongly and positively correlated with most of the environments as shown by the structure matrix (Table.30). The second weaker principal component usually explained the interactive effects of genotypes to winter and spring environments (winter and spring contrast). That is, there were moderate to low negative correlations between second component score and winter environment means, and strong positive correlations with late spring means in the structure matrix (Table 30).

Thus for each character used, there were generated two useful principal component scores for each genotype. The next step was to cluster these genotype scores into groups of similarly responding patterns. As described earlier, seven genotypes (six genotype did not reach to flowering in spring sowing, and genotype CROW 45 flowered very late with only a few fertile tillers in a row) were simply classified as a group with strong vernalization response, and separated. It was the rest of the genotypes which were classified using these procedures. From these, another five clusters were recognized (Figure 4.9).

The cluster means of the principal component scores were considered after clustering, to help in the interpretation of vernalization response and photoperiod sensitivity (Table 4.33). The definition of the clusters in terms of habit characteristics were based on the interpretation of the cluster means of principal component scores (Table 4.33) on one hand, and on the relevant hypotheses of growth habit which were reviewed and discussed earlier (chapter 2 and 5) on the other hand. In addition the cluster means of the characters were estimated to assist in understanding the clusters (Table 4.34).

The multivariate phenotypic analysis done in this study was ultimately successful in defining the plant types, and confirm the efficiency of the multiple character approach.

The identified groups and their included genotypes are listed now, and their general performances and interactive performances (winter X spring contrast) on the basis of four important characters (FLN, DFL, FRAT and SPKN) are summarized, as follows.

Group 1 (WW):

1. Avalon, 2. C3640, 3. CR3/135 4. CR3/136, 5. 3410-10, 6. 3413-09, 7. CROW 45

General performance: A large number of leaves and spikelets; late timing of flag leaf and low ratio of tiller fertility.

Winter X spring contrast: Vegetative phase and leaf appearance is continued till next growing season in spring sowing. Flag leaf does not unfold and the ratio of tiller fertility is almost near zero in spring sowing.

Definition: True winter wheats, with strong vernalization gene(s). Quite possibly they possess vrn1 allele(s).

Group 2 (Cluster 2):

1. 3665-0, 2. 722,02, 3. Konini, 4. 3665-30, 5. C7205 (CROW 17)

General performance: A large number of leaves and medium number of spikelets, medium late timing of flag leaf and relatively low ratio of fertile tillers.

Winter X spring contrast: Smaller number of leaves in spring than in winter,

more spikeles in spring than in winter, time to flag leaf (compared to others) is later in spring than in winter, tiller fertility ratio is larger in spring than in winter.

Definition: Facultative wheats, with moderate vernalization response and photoperiod sensitive. This tends to confirm Stelmakh (1987) that facultative or transitory wheats are genotypes with intermediate vernalization (possessing vrn2) in a photperiod sensitive back ground.

Group 3 (Cluster 4):

1. Genero 81, 2. Otane Rogue

General performance: Relatively low number of leaves and low number of spikelet, medium early timing of flag leaf and high ratio of fertile tillers.

Winter X spring contrast: Larger leaf number in spring than in winter, larger spikelet number in spring than in winter, time to flag leaf (compared to others) is later in spring than in winter, ratio of fertile tillers is about the same in spring and winter.

Definition: Semi spring type (spring type with moderate vernalization requirement) and insensitive to photoperiod.

Group 4 (Cluster 1):

1. PBI 1908-49-5 (CROW), 2. P648,05 (CROW), 3. PBI 1641-25, 4. P693,02, 5. 3496-03, 6. PBI 1908-49-7, 7. 3431-01, 8. PBI 1013-13-3
9. 88 PBI 9, 0. 3415-20, 11. 3494-01

General performance: A large number of leaves and large number of

spikelets, late timing of flag leaf, low ratio of fertile tillers.

Winter X spring contrast: Fewer leaves in spring than in winter, slightly lower number of spikelet in spring than in winter, time to flag leaf (compared to others) is earlier in spring than in winter, ratio of fertile tillers is higher in spring than in winter.

Definition: Spring wheats, with strong photperiod sensitivity and very week vernalization requirement.

Group 5 (Cluster 3):

1. Batten, 2. CRSW 18, 3. 3458-34, 4. CRSW (PSW 251), 5. CRSW -22, 6. Rongotea, 7. 44/102/1, 8. P694,03, 9. Oroua, 10. 659/16

General performance: A medium number of leaves and medium number of spikelets, medium early timing of flag leaf and relatively high ratio of fertile tillers.

Winter X spring contrast: Considerably fewer leaves in spring than in winter, much lower number of spikelet in spring than in winter, time to flag leaf (compared to others) is earlier in spring than in winter, ratio of fertile tillers is higher in spring than in winter.

Definition: Spring wheats, with strong photperiod sensitivity and no vernalization requirement.

Group 6 (Cluster 5):

1. 18-IBWSN-136, 2. Karamu, 3. Transvaal, 4. South Africa 1116, 5. CRSW 19, 6. 449,02/22, 7. Otane, 8. CR5/188/PSW251

General performance: A small number of leaves and relatively large number of spikelets, early timing of flag leaf and high ratio of tiller fertility.

Winter X spring contrast: Fewer leaves in spring than in winter, higher number of spikelets in spring than in winter, time to flag leaf (compared to others) is later in spring than in winter, ratio of tiller fertility is lower in spring than in winter.

Definition: Spring wheats, with weak vernalization requirement and no photoperiod sensitivity.

5.4 Implication for Wheat Breeding

5.4.1 Comparison Between Screening Mothods

It is useful to check the sensitivity or insensitivity to vernalization and photoperiod in individual genotype selected to be used in breeding programs. Because of the expense and the difficulty of evaluation of a large number of genotypes, in controlled conditions, screening of germplasm for this purpose in field conditions is important and useful for practical breeders in extensive breeding programs.

In most of the growth habit studies which have been done in controlled conditions (growth cabinet and green house) a small number of genotypes have been examined (Pugsley 1973; Rahman and Wilson 1977; Halse and Weir

1979; Flood 1983; Flood and Halloran 1984; Gotoh 1975). Practical breeding requires large number of genotypes to be examined for many relevant attributes under field conditions. This study is such a case. Some workers such as Davidson et al (1985) examined a large number of genotypes in controlled conditions, but they considered only ear emergence time.

However, because of comfounding of temperature and daylength in natural conditions (in the field), recognition of vernalization and photoperiod responses is not possible simply by considering one character, such as days to ear emergence. Here, thirteen characters were studied, and four of these were evaluated as the most responsive traits (namely LFN, DFL, FRAT and SPKN). These may be considered as key characters for screening studies of wheat genotypes, for the presence and magnitude of vernalization and photoperiod responses and subsequently plant type.

As discussed earlier usual univariate analysis of one character at a time was not useful to determine this responses under the complex field conditions. Therefore principal component analysis was done to ordinate univariate responses across environments, and then cluster analysis was used to join the characters multivariately to clalassify the genotypes (chapter 3).

5.4.2 Selection in Relation to Growth Habit

Wheat breeders manipulate usually the **Vrn** and **Ppd** genes unknowingly by selecting for the yield and adaptation characters such as earliness, large number of spikelets per spike, tillering capacity, high ratio of tiller fertility and

so on, which are influenced by vernalization and photoperiod sensitivity. On ther hand, the expected genetic advance in a selection program is determined by some factors described as follows:

$$\Delta G = ih^2\sigma^2_p$$

where: ΔG = response to selection (genetic advance)

i = selection intensity

h^2 = heritability of the character

σ^2_p = phenotypic variance

Since, the effectiveness of selection or genetic advance obtained by selection is dependent on heritability and phenotypic variation of a particular character, selection for attributes with low heritability and/or phenotypic variation would not be useful.

While the full heritability of most of the studied characters was very low to moderate, the phenotypic variation was considerably high for the G X E interactive characters used to classify the response patterns of the genotypes (Tables 4.6 and 4.8). It seems that selection for wheat type using characters: leaf number, spikelet number and the fertility ratio of tillers might be more effective than using flowering characters, because heritability of flowering characters was considerably lower (Table 4.8).

Genotypic correlation is also important in determining correlated selection responses, or even for indirect selection. The presence of very high and positive genotypic correlation between flowering and the number of leaves suggests that selection for flowering time and earliness using this characters would be effective. It should be noted that while character FRAT is more heritable than the other key characters, there is negatively high genotypic correlation between this trait and characters DFL, LFN and SPKN (Tables 4.6 and 4.8). Therefore, selection to increase FRAT would at the same time, tend to decrease leaf and

spikelet number and timing of flowering.

5.4.3 Adaptive Value of Vernalization and Photoperiod Sensitivity

Development of new cultivars adapted to various stress environments is an important part of the wheat breeding programs in the world. The results presented here may be useful for wheat breeders in designing cultivars with optimum adjustment to the environmental conditions.

Floral initiation in genotypes with strong vernalization is delayed in autumn sown wheat and consequently increase winter hardiness by minimizing the potentially winter freezing effect of temperature on the floral apex. Vernalization and photoperiod sensitivity increase wheat yield in favourable long growing conditions by increasing the number of leaves and consequently the number of spikelets and tillers (Potentially ears), (Tables 4.19, 4.22 and 4.24). The maximum yield in Northern Europe is obtained growing varieties with strong photoperiod sensitivity (Kirby and Appleyard 1987).

Davidson *et al* (1985) suggested that moderate to low vernalization response in Australian wheat could be used in adjusting flowering time to prevent frost and grazing damage.

Photoperiod and vernalization insensitivity alleles (Ppd and Vrn respectively) accelerate flowering time (Tables 4.15 to 4.17). These alleles are used to reduce the duration of growth cycle to escape the drought conditions in flowering time in water stress conditions. The international Wheat breeding program of CIMMYT produce photoperiod and vernalization insensitive varieties (e.g Karamu)to achieve earlier ear emergence for tropical and subtropical regions.

Regarding the importance of sowing date in regulating the nvironment and its highly significant effects on all recorded character (Chapter 4), The results of adaptation and stability trials may be significantly change by changing sowing from year to year or location to location.

Lateness in New Zealand wheat cultivars may be involved with photoperiod sensitivity genes rather than vernalization genes (Section 5.3). Using photoperiod sensitivity genes may increase wheat yield in New Zealand at least in North Island because of existence of a favourable long growing season.

CONCLUSIONS

1. Differences in the sample of genotypes and environments in the two sets of analyses gave different estimates of genotype, environment and genotype x environment variance components, and heritabilities, as expected. These results confirm the need to have unbiased samples and to use random-effect statistics.

2. Although the timing of development was physiologically related to the rate of leaf appearance and the rate of tiller production, selection for these characters may not be useful. This is because the observed genetic variation and heritability for these attributes was very low.

3. Leaf number and tiller fertility ratio were the most G X E interactive (the most responsive to the variation of temperature and daylength) and consequently the most useful characters to evaluate growth habit. The heritability estimates of these two characters were also higher than for flowering characters.

4. Presence of very high genotypic and phenotypic correlations between flowering characters, time to flag leaf, heading and anthesis indicated that these characters may be different performances of one physiological process. Any of these attributes can be an indicator of the timing of development, and the earliest event (flag leaf emergence) may be more appropriate for this purpose.

5. Leaf number is genotypically and phenotypically associated with flowering characters and spikelet number. This dependence, together with higher heritability and larger G X E interaction, suggests that using leaf number in selection for growth habit and timing of development may be more useful than using the other characters.

6. Vernalization response and photoperiod sensitivity varied quantitatively. This indicates that vernalization requirement and photoperiod sensitivity may be controlled by polygenes rather than one or few major genes. This could be subject to future studies.

7. The determination of the growth habit of the genotypes was done considering the joint pattern of several attributes in their responses across the environments. Using one character at a time for this purpose was not useful in the confounded conditions of temperature and deylength in field environments (sowing dates).

8. Principal component analysis was effective in analysing G X E means of the genotypes for seven G X E interactive characters.

9. The genotypes were classified using cluster analysis on the basis of their principal component scores. This was very successful in defining 5 clusters which corresponded well to various physiological discussions.

References

Aamodt, O. S. (1923). The inheritance of growth habit and resistance to stem rust in a cross between two varieties of common wheat. *J. Agric. Res.* **24,** 457-469 (Cited by Flood and Halloran 1986).

Aitken, Y. (1966). Flower initiation in Relation to Maturity in Crop Plants: III. The flowering response of early and late cereal varieties to Australian environments. *Aust. J. Agric. Res.* **17,** 1-15.

Aherns, J. F.; Loomis, W. E. (1963). Floral induction and development in winter wheat. *Crop Sci.* **3,** 463-466.

Allan, R. E.; Vogel O. A.; Peterson, C. J. (1962). Seedling emergence of rate of fall sown wheat and its association with plant height and coleoptile length. *Agron. J.* **54,** 347-350.

Allard, R. W. (1960) Principales of Plant Breeding. John Wiley and Sons Inc. New york and Lodon.

Anderberg, M. R. (1973) Cluster analysis for applications. Academic Press. New York.

Anonimous. (1988) SAS/STAT user's guide. SAS Institute Inc.

Ashraf, C. M.; Abu-Shakra. (1978). Wheat Seed Germination under low temperature and moisture stress. *Agron. J.* **70,** 135-139.

Baker, C. K.; Gallagher, J. N. (1983a). The development of winter wheat in the field.1. Relation between apical development and plant mophology. *J. Agric. Sci.* **101,** 327-335.

Baker, C. K. ; Gallagher, J. N. (1983b). The development of winter wheat in the field, 2. The control of primordium initiation rate by temperature and photoperiod. *J. Agric. Sci., camb.* **101,** 337-344.

Baker, C. K. ; Gallggher, J. N.; Monteith, J. L. (1980). Daylength change and leaf appearance in winter wheat. *Plant, Cell Environ.* **3,** 285-287.

Baker, J. T.; Pinter, P. J.; Reginato, Jr R.; Kanemasu, E. T. (1986). Effects of Temperature on leaf appearance in spring and winter wheat Cultivars. *Agron. J.* **78,** 605-613.

Baker, R. J. (1986) Selection Indices in Plant Breeding. CRC Press Inc. Florida.

Barnard, C. (1964) Form and structure. in *Grasses and Grassland.* (Ed. by Barnard, C.) Macmillan. London.

Becker, H. C.; Leon, J. (1988). Stability analysis in plant breeding. *Plant Breeding.* **101,** 1-23.

Berry, G. J.; Salisbury, P. A.; Halloran, G. M. (1980). Expression of vernalization in near isogenic wheat lines : duration of vernalization period. *Ann. Bott.* **46,** 235-241.

Bhat, S. R.; Goud,, J. V. (1979). Monosomic analysis of some morphological characters in wheat (*Triticum aestivum* L. em. Thell.). *Wheat Information Service,* **50,** 14-17.

Bidinger, F. R.; Witcombe, J. R. (1989) Evaluation of specific drought avoidance traits as selection criteia for improvement of drought resistance. in *Drought Resistance in Cereals.* (Ed. by Baker, F. W. G.) C.A.B. International. UK.

Blum, A. (1988). Plant Breeding for Stress Environments. CRC Press Inc, Florida.

Boatwrite, G. O. ; Ferguson, H. (1967). Influence of primary and/or adventitions root systems on wheat production and nutrient uptake. *Agron. J.* **59,** 299-302.

Boozini, A.; Giorgi, B. (1971). Genetic analysis of tetraploid and hexaploid wheat by utilization of monopentaploid hybrids. *Theor. Appl. Genet.* **41,** 67-74.

Briggle L. W.; Curtis B. C. (1987) Wheat worldwide. in *Wheat and wheat improvement.* (Ed. by Heyne E. G.) American Society of Agronomy. USA.

Brooking, I. R.; Kirby, E. J. M. (1981). Interrelationships between stem and ear development in winter wheat: the effects of A norin 10 dwarfing gene, Gai/Rht2. *J. Agric. Sci.* **97,** 37-381.

Brouwer, R. (1966) Root growth of grasses and cereals. in *The Growth of Cereals and Grasses.* (Ed. by Milthorpe, F. L.; Ivins J. D.) pp. 153-163. Butterworths. London.

Byth, D. E.; Eiseman, R. L.; Delacy, I. H. (1976). Two way pattern analysis of a large data set to evaluate genotypic adaptation.*Heredity.* **37,** 215-230.

Cao, W.; Moss, N. D. (1991). Vernalization and phyllochron in witer wheat. *Agron. J.* **83,** 178-179.

Chuard, P. (1960). Vernalization and its relations to dormancy. *Ann. Rev. Plant physiol.* **11,** 119-238.

CIMMYT, (1989). Annual Report (1987-988), Wheat. CIMMYT, Mexico.

Chujo, H. (1966a). Difference in vernalization effect in wheat under various temperatures. *Proc. Crop Sci. Soc. Japan.* **35,** 177-186.

Chujo, H. (1966b). The effect of diurnal variation of temperature on vernalization in wheat. *Proc. Crop Sci. Soc Japan.* **35,** 187-194.

Le Clerg, E. L.; Leonard, W. H.; Clark, A. G. (1962) Field Plot Technique. Burgess, Minneapolis, Minn.

Cockerham, C. C. (1963) Estimation of genetic variances. in *Statistical Genetics and Plant Breeding*. (Ed. by Hanson, W. D. and Robinson, H. F.) pp. 53-94. NAS-NRC Pub.

Comstock, R. E.; Moll, R. H. (1963) Genotype-environment interactions. in *Statistical Genetics and Plant Breeding*. (Ed. by Hanson, W. D.; Robinson, H. F.) pp. 164-96. NAS-NRC Pupl.

Comstock, R. E.; Robinson, H. F. Genetic parameters, their estimation and significance. in *Proc. 6th Int. GrasslandCongress*. pp. 284-291.

Cooly, W. W.; Lohnes, P. R. (1971). Multivariate data analysis. Wiley. New York.

Cooper, J. P. (1960). Short day and low temperature induction in Lolium. *Ann. Bot.* **24,** 232-246.

Cormack, R. M. A review of classification. *JR. Stats. Soc.* **A 134,** 321-358.

Crump, S. L. (1946). he estimation of variance components in analysis of variance. *Biometrics.* **2,** 7-11.

Cullen, C. (1981) Pattern analysis of genotype X environment interactions and comparisons with alternative analyses. Massey University. New Zealand.

Davidson, J. L.; Christian, K. R.; Jones, D. B.; Brenner, P. M. (1985). Response of wheat to vernalization and photoperiod. *Aust. J. Agric. Res.* **36,** 347-359.

Delecolle, R.; Hay, R. K. M.; Guerif, M.; Pluchard, P.; Varlet, C. (1989). A method of describing progress of apical development in wheat, based on the time-course of organogenesis. *Field Crops Res.* **21,** 147-160.

Derara, N. F.; Marshall, D. R.; Balaam, L. M. (1969). Genetic variability in root development in relation to drought tolerance in spring wheats. *Exp. Agric.* **5,** 327-337.

Dolgusin, D. A. (1935). The world's collection of wheats on the backgroun of vernalization. Seljhozgiz, Moskva. Cited by Flood (1983).

Draper, N.; Smith, H. (1966) Applied Regression Analysis. John Wiley and Sons, Ltd. New Yourk.

Ehdaie, B.; Waines. J. G. (1989). Genetic variation, heritability and path analysis in landrases of bread wheat from southestern Iran. *Euphytica.* **41,** 183-390.

Eiseman, R. L.; Byth, D. E.; Delacy, I. H.; Taylor, P. J. (1977) A new approach to the analysis of genotypic adaptation and genotype-environment interactions. in *3rd SABRAO Proceedings.* pp. 3(d)-41-3(d)-47.

Evans, L. T. (1987). Short day induction of inflorescence initiation in some winter wheat varieties. *Aust. J. Plant Pysiol.* **14,** 277-286.

Evans L. T.; Bhatt, G. M. (1977). Influence of seed size, protein content and cultivar on ealy seedling vigour in wheat. *Canad. J. Plant Sci.* **57,** 929-935.

Evans, L. T.; Bingham, J.; Roskams, M. A. (1972). The pattern of grain set within ears of wheat. *Aust. J. Biiol. Sci.* **25,** 1-8.

Evans, L. T.; Wardlaw, I. F.; Fisher, R. A. (1975) Wheat. in *Crop physiology, some case histories.* (Ed. by Evans, L. T.) pp. 101-149. Cambridge University Press. Uk.

Everitt, B. (1974) Cluster analysis. Social Science Research Council. London.

FAO. (1983). Production Yearbook, 1982. **36,** 320.

Fitter, A. H.; Hay, R. K. M. (1981) Environmental physiology of plants. Academic Press. New York.

Federov, A. K. (1989). Physiological-Genetical basis for the type of plant development and length of the vegetation period in wheat. *Cereal Res.Comm.* **17(2),** 121-127.

Flood, R. G. (1983) Genetics and Physiology of Vernalization Response in Wheat. Ph.D thesis, University of Melbourne, Melbourne.

Flood, R. G.; Halloran G. M. (1984). The association of vernalization and photoperiod in wheat. *Cereal Res. comm.* **12(1),** 5-11.

Flood, R. G. ; Halloran, G. M. (1986). genetic and physiology of vernalization response in wheat. *Adv. In Agron.* **39,** 89-125.

Ford, M. A.; Austin, R. B.; Angus, W. J. (1981). Relationships between responses of spring wheat genotypes to temperature and photoperiodic treatments and and their performance in the field. *J. Agric. Sci.* **96,** 623-634.

Freeman, G. H. (1973). Statiscal methods for the analysis of genotype-environment interactions. *Heredity*. **31,**339-354.

Friend, D. J. C. (1965). Tillering and wheat production in wheat as affected by temperature and light intensity. *Can. J. Bot.* **43,** 1063-1076.

Friend, D. J. C.; Helson, V. A.; Fisher, J. E. (1962). Leaf growth in Marquis wheat, as regulated by temperature, light intensity, and day length. *Canad. J. Bot.* **40,** 299-311.

Gallagher, J. N. (1979). Studies of leaf growth, Interoduction and expansion in relation to temperature and ontogeny. *J. Exp. Bott.* **30,** 625-636.

Gallagher, J. N.; Biscoe, P. V.; Wallace, J. S. (1979). Field studies of leaf growth, winter wheat leaf expansion in relation to temperature and leaf water status. *J. Exp. Bott.* **30,** 657-688.

George, D. W. (1982). The growing point of fall sown of wheat: A useful measure of physiologic development. *Crop Sci.* **22,** 235-239.

Gordon, I. L. (1991). Computer Program THWAITE. Massy University, New Zealand. (Unpublished)

Gordon, I. L. (1991). Determination of Cutt-off point in cluster analysis. Massy University, New Zealand. (Pers. Com.)

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

Gotoh, T. (1976). Studies on varietal differences in vernalization requirement in wheat. *Jpn. J. Breed.* **26(4),** 307-327.

Gotoh, T. (1977). Intermediate growth habit wheat lines developed from a cross between spring and winter types. *Jpn. J. Breed.* **27(2),** 98-104.

Gotoh, T. (1979). Genetic studies on Growth habit of some important Spring wheat cultivars in Japan, with special references to the identification ofthe spring genes involved. *Jpn. J. Breed.* **29(2),** 133-145.

Gotoh, T. (1980). Gene analysis of degree of vernalization requirement in winter wheat. *Jpn. J. Breed.* **30(1),** 1-10.

Gotoh, T. (1983). Varietal variation and inheritance mode of vernalization requirement in common wheat. *Proc. 6th Int. Wheat Genetics Symp., Kioto, Japan.* 475-478.

Gott, M. B. (1961). Flowering of Australian wheats and its relation to frost injury. *J. Agric. Sci.* **12,** 547-565.

Gott, M. B. (1957). vernalization of green plants of winter wheat. *Nature.* **180,** 714-715.

Gregory, F. G.; purvis, O. N. (1948). Reversal of vernalization by high temperature. *Nature.* **161,** 859-860.

Griffing, B. (1956). Concept of general and specific combining ability in relation to diallel crossing system. *Aust. J. Biol. Sci.* **9,** 463-493.

Griffiths, F. E. W.; Lyndon, R. F.; Bennett, M. D. (1985). The effects of vernalization on the growth of the winter wheat shoot apex. *Ann. Bot.* **56,** 501-511.

Halloran, G. M. (1967). Gene dosage and vernalization response in homoeologous group 5 of Triticum aestivum. *Genetics.* **57,** 401-407.

Halloran, G. M. (1975). Genotype differences in photoperiodic sensitivity and vernalization response in wheat. *Ann. Bot.* **39,** 845-851.

Halloran, G. M. (1976). genes for vernalization response in homeologous group 5 of Triticum aestivum. *Can. J. Genet. Cytol.* **18,** 211-216.

Halloran, G. M. (1977). Developement basis of maturity differences in spring wheat. *Agron. J.* **69,** 899-902.

Halloran, G. M.; Boydell, C. V. (1967). Wheat chromosomes with genes for vernalization response. *Can. J. Genet. Cytol.* **9,** 632-639.

Halloran, G. M.; Pannenell, A. L. (1982). Duration and rate of development phases in wheat in two environments. *Ann. Bot.* **49,** 115-121.

Halse, N. J.; Weir, R. N. (1970). Effects of vernalization, photoperiod and temperature on phenological development and spikelet number of Australian wheat. *Aust. J. Agric. Res.* **21,** 383-393,

Halse, N. J.; Weir, R. N. (1974). Effects of temperature on spikelet number of wheat. *Aust. J. Agric. Res.* **25,** 687-695.

Hanson, W. D. (1963). Heritability, in *Stasitical Genetics and Plant Breeding.* (Ed. by Hanson, W. D.; Robinson, H. F.) pp. 125-139. NAS-NRC Publ. USA.

Haun, J. R. (1973). Visual qualification of wheat development. *Agron. J.* **65,** 116-119.

Hay, R. K. M.; Delecolle, R. (1989). The seting of rates of development of wheat plants at crop emergence: Influence of the environment on rates of leaf appearance. *Ann. APPl. Biol.* **115,** 333-341.

Hay, R. K. M.; Kemp, D. R. (1990). Primordium initiation at the stem apex as the primery evnt controling plant development: perliminary evidence from wheat for the regulation of leaf development. *Plant, Cell and Env.* **13,** 1005-1008.

Hay, R. k. M.; Kirby E. J. M. (1991). Convergence and syncrony-a review of the coordination of development in wheat. *Aust. J. agric. res.* **42,** 661-700.

Hay, R. K. M.; Tunnicliffe Wilson, G. (1982). Leaf appearance and extension in field-grown winter wheat plants: the importance of soil temperature during vegetative growth. *J. Agric. Sci.* **99,** 403-410.

Hay, R. K. M.; Walker, A. J. (1989) An introduction to the physiology of crop yield. Longman. UK.

Hill, J. (1975). Genotype-environment interactions -a challenge for plant breeding. *J. Agric. Sci.* **85,** 477-493.

Holmes, D. P. (1973). Inflorescence development of semidawrf and standard height wheat cultivars in different photoperiod and nitrogen treatments. *Can. J. Bot.* **51,** 941-956.

Hoogendoorn, J. (1984) Variation in time of ear emergence of wheat (Triticum aestivum L.): Physiology, genetics and consequences of yield. Wageningen.

Hsu, p.; Walton, P. D. (1970). The inheritance of morphological and agronomic charcters in spring wheat. *Euphytica.* **19,** 54-60.

Hunt, L. A. (1979). photoperiodic response of winter wheats from different climatic regions. *Pflanzenzudrg.* **82,** 70-80.

Ishihara, A. (1963). Physilogical studies on the vernalization of wheat plants. IV. The effetcs of temperature and photoperiod on the progress of vernalization in growing plant. *Proc. Crop Sci. Soc. Japan.* **31,** 297-308.

Jedel, P. E.; Evans, L. E.; Scrath, R. (1986). vernalization responses of selected group of spring wheat(Triticum aestivum L.) cultivars. *Can. J. Plant Sci.* **66,** 1-9.

Jones, H. G. (1985). Adaptive significance of leaf development and structural responses to environment. in *Control of leaf growth.* (Ed. by Baker, N. R.; Davise, W. J.; Ong, C. K.) pp. 155-173 Cambridge University Press. Uk.

Kato, K.; Ikoma, H.; Hayashi, K. (1987). Geographical distribution of the genes for vernalization response and its implication for the adaptability of wheat. *Proc. 7th Int. Wheat Genet. Symp. Cambridge.* 533-539.

Kato, K.; Tono, S.; Yamazaki, S.; Hayashi, K. (1990). Simplified culture method of detached ears and its application to vernalization in wheat. *Euphytica.* **49,** 161-168.

Kihara, H.; Tanaka, M. (1958). Morphological and physiological variation among Aegilops squarrosa strains collected in Pakistan, Afganistan and Iran. *Preslia.* **30,** 241-251.

Kirby, E. J. M. (1974). Ear development in spring wheat. **J. Agicr. Sci. 82,** 437-447.

Kirby, E. J. M. (1988). Analysis of leaf, stem and ear growth in wheat from terminal spikelet stage to anthesis. *Field Crops Res.* **18,** 127-140.

Kirby, E. J. M. (1990). Co-ordination of leaf and spikelet primordium initiation in wheat. *Field Crops Res.* **25,** 253-264.

Kirby, E. J. M.; Appleyard, M. (1984). Cereal Development Guide 2nd edn. The N.A.C. Araable unit, Plan Breeding Institute, England.

Kirby, E. J. M.; Appleyard, M. (1987). Development and structure of the wheat plant. in *Wheat Breeding, its scientific basis.* (Ed. by Lupton, F. G. H.) pp. 287-311. Chapman and Hall Ltd. London, New York.

Kirby, E. J.; Appleyard, M.; Fellowes, G. (1982). Effects of sowing date on the temperature response of leaf emergence and leaf size in barley. *Plant, Cell and Environment.* **5,** 477-484.

Kirby, E. J.; Appleyard, M.; Fellowes, G. (1985). Effects of sowing date and variety on main shoot leaf emergence and number of leaves of barley and wheat. *Agronomie.* **5,** 117-126.

Kirby, J. M.; Perry, M. W. (1987). Leaf emergence rate of wheat in a mediterranian environment. *Aurt. J. Agric. Res.* **38,** 455-465.

Kirby, J. M.; Porter, J. R.; Day, W.; Adam, J. S.; Appleyard, M.; Ayling, S., Baker, C. K.; Belford, r. K.; Chapman, A.; Fuller, M. P.; Hampson, J.; Hay, R. K. M.; Matthews, S.; Thompson, W. J.; Weir, A. H.; Willington V. B. A.; Wood, d. W. (1987). An analysis of primordium initiation in Avalon winter wheat crops with different sowing dates and at ten sites of England and Scotland. *J. Agicr. Sci.* **109,** 123-134.

Klaimi, Y. Y.; Qualset, C. O. (1973). Genetics of heading time in wheat (Triticum aestivum), I. The iheritance of the photoperiodic response. *Genetics.* **74,** 139-156.

Klaimi, y. Y.; Qualset, C. O. (1974). Genetics of heading time in wheat (Triticum aestivum). II. The inheritance of vernalization response. *Genetics.* **76,** 119-133.

Knott, D. R. (1959). The inheritance of rust resistance. IV. Monosomic analysis of rust resistance and some other charaters in six varieties of wheat including Gabo and Kenya Farmer. *Can. J. Plant Sci.* **39,** 215-228.

Kuspira, J.; Unrau, J. (1957). Genetic analyses of certain characters in common wheat using whole chromosome subtraction lines. *Can. J. Plant Sci.* **37,** 300-326.

Krekule, J. (1987). Vernalization in wheat. in *Manipulation of Flowering.* (Ed. by J. G. Atherton) pp. 159-169. Butterworths, London

Langer, R. H. M.; Hainf, M. (1973). A study of floret development in wheat (Triticume aestivuem). *Ann. Bot.* **37,** 743-751.

Law, C. N. (1966). The location of genetic factors affecting a quantitative character in wheat. *Genetics.* **53,** 487-498.

Law, C. N. (1972). The analysis of inter-varietal choromosome substitutions in wheat and their first generation hybrids. *Heredity.* **28,** 169-179.

Law, C. N. (1987). The genetic control of day-length response in wheat. in *Manipulation of Flowering.* (Ed. by J. G. Atherton) pp. 225-240. Butterworths, London.

Law, C. N. ; Sutka, J.; Worland, A. J. (1978). A genetic study of day-length response in wheat. *Hereaditry.* **41 (2),** 185-191.

Law, C. N.; Worland, A. J.; Giorgi, B. (1976). The genetic control of ear-emergence time by chromosomes 5A and 5D of wheat. *Heredity.* **36,** 49-51.

Lefkovitch, L. P. (1985). Multi-criteria clustering in genotype-environment interaction rpoblems. *Theor. Appl. Genet.* **70,** 585-589.

Levy, J. Peterson, M. L. (1972). Responses of spring wheat to vernalization and photoperiod. *corp Sci.* **12,** 487-490,

Li, X. Z.; Hao, N. B.; Tan, K. H. (1988) Changes of soluble protein components in winter wheat (Triticum aestivum) shoots during vernalization and their relation to morphogenesis, *Wheat, Barley and Triticale Abstracts*, C. A. B.

Lin, C. S.; Binns, M. R.; Lefkovitch, P. (1986). Stability analysis: Where do we stand? *Crop Sci.* **26,** 894-900.

Lin, J. T.; Stafford, A. E. (1987). Comparison of the endogenous gibbrellins in the shoots and roots of vernalized and non-vernalized chinese spring wheat seedlings. *Phytochemistry.* **26(9),** 2485-2488.

Masle, J. (1985) Competition amongst tillers in winter wheat: Consequences for growth and development of the crop. in *Wheat Growth and Modeling.* (Ed. by Day, W.; Atkin, R. K.) pp. 33-54. Plenum Press. New York.

Masle, J.; Doussinault, G.; Sun, B. (1989). Response of wheat genotypes to temperature and photoperiod in natural conditions. *Crop Sci.* **29,** 712-721.

Mather, K. (1949) Biometrical genetics. Methuen, London.

Mather, K.; Jinks, J. L. (1982) Biometrical Genetics, 3rd edn. Chapman and Hall. London.

Mayestrenko, O. I. (1974). Identification of choromosomes carrying genes Vrn1 and Vrn3 inhibiting winter habit in wheat. *European Wheat Aneuploid Co-operative Newsletter.* **4,** 49-52.

Mayestrenko, O. I. (1980). Cytogenetic study of growth habit and ear emergence time in wheat (*Triticum aestivum* L.). In *well-being of mankind and genetics. Proc. XIV Int. Cogr. Genet.,* **1,** 267-282. Mir, Moskow.

Mcintosh, R. A. (1973). A catalogue of gene symbols for wheat. *Proc. 4th Int. Wheat Genet. Symp.* 893-937.

McKinney, H. H.; Sando, W. J. (1933). Earliness and seasonal growth habit in wheat as influenced by temperature and photoperiodism. *Jour. Heredity.* **24,** 169-179.

Miltothorpe, F. L.; Moorby, J. (1979). An Introduction to Crop Physiology 2nd edn. Cambridge University Press, London.

Morrison, D. F. (1967) Multivariate Statistical Methods. McGraw-Hill. USA.

Napp-Zinn, K. (1987). Vernalization-Environmental and genetic Regulation. in *Manipulation of Flowering.* (Ed. by J. G. Atherton) pp. 123-132. Butterworths, London.

O'Brien, L. (1978). Effects of root media on growth of wheat seminal roots. *Crop Sci.* **18,** 685-687.

Paldi, E.; Devay, M. (1977). Ribosomal RNA synthesis in spring and winter wheat varieties at temperature active for vernalization and at natural and devernalization temperatures. *Biochemie und physioloie der pflanzen,* **171,** 249-259. Cited by Krekule (1987).

Passiora, J. B. (1972). The effect of root geometry on the yield of wheat growing on stored water. *Aust. J. Agric. Res.* **23,** 745-752.

Patrick, J. W. (1972). Distribution of assimilate during stem elongation in wheat. *Aust. J. Biol. Sci.* **25,** 455-467.

Peacock, J. M. (1975). Temperature and leaf growth in *Lolium perenne.* 2. The site of temperature peception. Journal of Applied Ecology **12,** 115-1213.

Perry, M. W.; Siddique, K. h. M. (1987). Predicting phenological development for Australian wheats. *Aust. J. AgricRes.* **38,** 809-819.

Peterson, C. M.; Kleeper, B.; Rickman, R. W. (1982). Tiller development at the coleoptilar node in winter wheat. *Agron. J.* **74,** 781-784.

Poehlman, J. M. (1979) Breeding Field Crops, Seconed edition. AVI publishing Co. INC. USA.

Pugsley, A. T. (1963). The inheritance of a vernalization response in Australian spring wheat. *Aust. agric. res.,1963,.* **14,** 622-627.

Pugsley, A. T. (1965). Inheritance of a correlated day-length response in spring wheat. *Nature.* **207,** 108.

Pugsley, A. T. (1966). The photoperiodic sensitivity of some spring wheats with special reference to the variety Thatcher. *AustJ. Agric. Res.* **17,** 591-599.

Pugsley, A. T. (1968). Genetic studies of phasic development and their application to wheat breeding. *Proc. 3rd Int. Wheat Genet. Symp.* 288-293.

Pugsley, A. T. (1971). A genetic analysis of spring-winter habit of growth in wheat. *Aust. J. Agric. Res.* **22,** 21-31.

Pugsley, A. T. (1972). Additional genes inhibiting winter habit in wheat. *Euph.* **21,** 547-552.

Pugsley, A. T.; Warrington, I. J. (1979). Developmental patterns in standard and semi-dwarf wheats. *Australian Plant Breeding and Genetics Newsletter.* **29,** 39-40.

Quizenberry, J. E. (1982). Breeding for drought resistance and plant water use efficiency. in *Breeding Plant for Less Favorable Environments.* (Ed. by Christiansen, M. N.; Lewis, C. F.), John Wiley and Sons, New York, Toronto.

Rahman, M. N. ; Wilson, J. H. (1977). Determination of spikelet number in wheat. I Effect of varying photoperiod on ear development. *Aust. J. Agric. Res.* **28,** 565-574.

Rawson, H. M. (1971). Tillering Patterns in wheat with special references to the shoot at the coleoptile nodes. *Aust. J. Biol. Sci.* **24,** 829-841.

Reddy, L. V.; Matzger, R. J.; Ching, T. M. (1985). Effect of temperature on seed dormancy of wheat. *Crop Sci.* **25,** 455-458.

Rees, A. R. (1987). Environmental and genetic regulation of photoperiodism -a review. in *Manipulation of Flowering.* (Ed. by J. G. Atherton) pp. 187-202. Butterworths, London.

Riddell, J. A.; Gries, G. A. (1958a). Development of spring wheat. II. The effect of temperature on response to pohotoperiod. *Agron. J.* **50,** 739-742.

Riddell, J. A.; Gries, G. A. (1958b). Temperature of maturation and age seeds as factors infuencing their response to vernalization. *Agron. J.* **50,** 743-746.

Robinson, H. F.; Comstock, R. E.; Harvey, P. H. (1941). Estimates of heritability and degree of dominance in corn. *Agron.J.* **41,** 353-359.

Salisbury, F. B. (1963) The flowering process. Pergamon. London.

Satterthwaite, F. E. (1946). An approximate distribution of estimates of variance components. *Biometrics Bull.* **2,** 110-114.

Scarth, R.; Kirby, E. J. M.; Law, C. N. (1985). Effects of the photoperod genes Ppd1 and Ppd2 on growth and development of the shoot apex in wheat. *Ann. Bot.* **55,** 351-359.

Scarth, R.; Law, C. N. (1983). The location of the photoperiod gene Ppd1 gene Ppd2 and an additional genetic factor for ear emergence time on chromosome 2B of wheat. *Heredity.* **51,** 607-619.

Scarth, R.; Law, C. N. (1984). The control of day length response in wheat by the group 2 chromosomes. *Zetischrift Pflanzenzuchtung.* **92,** 140--150.

Schlehber, A. M.; Tucker, B. B. (1967) Culture of wheat. in *Wheat and Whea Improvement.* (Ed. by Quisenberry, K. S.; Reitz L. P.) Amer. Soc. Agron. Madison.

Sereeprasert, V. (1990) Quantitative inheritance studies of grain Maturation and germination in three wheat crosses. Ph.D thesis, Massey University. New Zealand.

Sibbony, M.; Pinthus, M. J. (1988). Floret initiation and development in sprin wheat (Triticum aestivum L.). *Ann. Bot.* **61,** 473-479.

Siddique, K. H. M; Kirby, E. J. M; Perry, M. W. (1989). Earstem ratio in old and modern wheat varieties: relationship with improvement in number of grain per ear and yield. *Field Crops Res.* **21,** 59-78.

Simmonds, N. W. (1979) Principales of Crop Improvement. Longman Group Ltd. London and New Yourk.

Simmons S. R. (1987) Growth, development and physiology. in *Wheat and wheat improvement*. (Ed. by Heyne E. G.) American Society of Agronomy. USA.

Simons, R. G. (1982). Tiller and ear production of winter wheat. *Field Crops Abst.* **35,** 213-224.

Singh, H.; Jener, C. F. (1983). Culture of detached ears of wheat in liquid culture: Modification and extension of the method. *Aust. J. Plant Pysiol.* **10,** 227-236.

Singh, M. P. (1967). Monosomic analysis in wheat. *Heredity.* **22,** 591-596.

Snape, J. W. (1987) Conventional method of genetic analysis in wheat. in *Wheat Breeding, its scientific basis.* (Ed. by Lupton, F. G. H.) pp. 111-127. Chapman and Hall Ltd. London, New York.

Snape, J. W.; Law, C. N.; Worland, A. J. (1976). Chromosome variation for loci controlling ear emergence time on chromosome 5A of wheat. *Heredity.* **37,** 335-340.

Snape, J. W.; Law, C. N. ; Young, C. F.; Worland, A. J. (1979). Genetical analysis of chromosome substitution lines of bread wheat using second generation hybrids. *Heredity.* **42,** 247-258.

Spitters, C. J. T. ; Kramer, TH. (1986). Differences between spring wheat cultivars in early growth. *Euph.* **35,** 273-292.

Steel, R. G. D.; Torrie, J. H. (1980) Principles and procedures of statistics, A biometrical approach 2nd edn. McGraW-Hill. International.

Stelmakh, A. F. (1987). Growth habit in common wheat, (*Triticum aestivum* L. EM. Tell.). *Euph.* **36,** 513-519.

Stern, W. R.; Kirby, E. J. (1979). Primordium initiation at the shoot apex in four contrasting vaieties of spring wheat in response to sowing date. *J. Agric. Sci.* **93,** 203-215.

Strand E. (1989). Studies on seed dormancy in small grain species.II. Wheat. Norwegian . *Journal of Agricultural Sciences.* **3,** 101-105.

Suge, H.; Yamada, n. (1965). flower promoying effect of gibberallin in winter wheat and barley. *Plant and Cell Physiol.* **6,** 147-160.

Sutka, J.; Kovacs, G.; Galiba, G.; Koszegi, B. (1987). Sbstitution analysis of frost resistance in wheat callus culture. *Proc. 7th Int.Wheat Genet. Symp.* **2,** 891-894.

Takahashi, H.; Yasuda, S. (1970). Genetics of earliness and growth habit in barley . *In Barley Genetics. Proc. 2nd Int. Barley Genet. Symp.* **II.,** 388-408.

Tan, K. H.; Wang, W. H.; He, H. W.; Li, S. Q. (1981). Effect of metabolic inhibitors on the vernalization process in winter wheat. *Acta Botanica Sinica.* **23,** 371-376.

Tanaka, M. (1956). Spring and winter-growing habit in Aegilops squarrosa var. Typica. *Wheat Information Servise.* **3,** 22.

Tanaka, M. (1959). Growing habit of *Aegilopsis squarrosa* stains in Afghanistan and Iran. *Wheat Information Sevice.*, **8,** 6-8.

Tanaka, M.; Yamashita, K. (1957). Growing habit of Aegilopsis squarrosa stains collected in Pakistan, Afghanistan and Iran. *Wheat Information Sevice.* **6,** 18-19.

Teow, S. H. (1978) Evaluation of variability in a Fog grass gene pool. M.Ag.Sc. thesis, Massey Unversity. New Zealand.

Thorn, G. N.; Wood D. W. (1988). Contribution of shoot categories to growth and yield of winter wheat. *J. Agric. Sci.* **111,** 285-294.

Trione, E. J.; Metzger, R. J. (1970). Wheat and Barley Vernalization in a precise temperature gradient. *Crop Sci.* **10,** 390-392.

Tsunewaki, K. (1966). Comparative gene analysis of common wheat and its ancestral species. II. Waxiness, growth habit and awnedness. *Jap. Journ. Bot.* **19,** 175-229.

Tsunewaki, K. (1968). Origin and phylogenetic differentiation of common wheat revealed by comparative gene analysis. *Proc. 3rd Int. Wheat genet. Symp.* 71-85.

Vavilov, N. I. (1951). The origin, variation immunity and breeding of cultivated plants. Translated by K. S. Chester. The Ronald Press Company, New York.

Wall, P. C.; Carttwright, P. (1974). Effects of photoperiod, temperature and vernalization on the phenology and spikelet numbers of spring wheat. *Ann. APPl. Biol.* **76,** 299-309.

Weir, A. H.; Bragg, P. L.; Porter, J. R.; Bayner, J. H. (1984). A winter wheat crop simulation model without water or nutrint limitations. *J. Agric. Sci.* **102,** 371-382.

Welsh, J. R.; Keim, D. L.; Pirasteh, B.; Richards, R. D. (1973). Genetic control of photoperiodic response in wheat. *Proc. 4th. Int. Wheat Genetics Symposium.* 879-884.

Westcott, B. (1986). Some method of analysing genotype-environment interaction. *Heredity.* **56,** 243-253.

Westcott, B. (1987) Yield assesment. in *Wheat Breeding, its scientific bais.* (Ed. by Lupton, F. G. H.) pp. 339-368. Chapman and Hall Ltd. London, New York.

Williams, R. F. (1960). The physiology of growth in the wheat plant. I. Seedling growth and the pattern of growth at the shoot apex. *Aust. J. Biiol. Sci.* **13,** 401-428.

Worland, A. J.; Gale, M. D.; Law, C. N. (1987) Wheat Genetics. in *Wheat Breeding, its scientific basis.* (Ed. by Lupton, F. G. H.) pp. 129-171. Chapman and HAll Ltd. London, New York.

Appendix 1.1 Pedigree of examined germplasm

Genotype	Pedigree
Batten	Grifin/843-01//Kafkaz///Siete Cross -66/Cross-7.61//Inia-66/Kopora
C7205 (CRAW 17)	C1.2.3.1//R11.3/Courtot
PBI 1908-49-5	SW1031-132/Sicco
P648.05 (CROW 50)	61.01/BN3447
PBI 1908-49-7	SW1031-132/Sicco
C3640	RC72.485/RC72.483//RC72.450/DC3CN
P693-02	79WL 441/2/Otane
PBI1013.13.3	CML 51/Bounty
3431-01	Oroua/Olympic
3458-34	TW275.7.6.10/Oroua
3494-01	Oroua/Cook/343.01
88PBI9	TAS 894.5.3/Sicco
Avalon	Maris Ploughman/Bilbo
CR3-135	Maris Hobbit/2278.01
CR3-136	TL 365 Q.34/Takahe
CRAW 45	Hustler/2654.01
PBI 1641-25	TAS 894.53/Salitaire "sib"
3415-20	TQS 39.79.7.3/Oroua
3410-10	Bounty/CR3.136
3413-09	Narwan/CR3.136
Konini	Fortuna/Arawa.9//1022.01/713.01

Appendix 1.1 continued

Genotype	Pedigree
3496-03	TQS39.79.7.3/65.09//Konini
3665-30	Mission/Konini
3665-08	Mission/Konini
Otane	Tobari 's'/Napo//Noroeste-66/Ira/// Bluebird/Gallo
CR5/188 (PSW 251)	Karamu/UQ139
CRSW 6 (PSW 251	65.09//II-62-1/3/Karamu
CRSW 18	(694.01) 79WL 446/2/Otane
CRSW 19	(693.01) 79WL 441/2/Otane
CRSW 22	(648.04) 61.01/BN3447
Genero-81	Kavkaz/Buho's'//Kalyasona/Bluebird
18-IBSWN	Bobwhite's'/Very's'
P694,03	79WL 446/2/Otane
Oroua	66RN395/Skemes
Karamu	Lerma Rojo/Norin-10-Brevos/3/Ardes Enano
Rongotea	Raven/66RN430
Otane Rogue	See Otane
Transvaal	?
Sout Africa 1116	?
659/16	Otane/64.02
449.02.22	Oroua/65.09
441.02.1	65.09/Skemer
722,02	Tiritea/Otane